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**POPULATION DYNAMICS OF THE SUB-ARCTIC COPEPOD  
*CALANUS FINMARCHICUS* IN THE GULF OF MAINE:  
DEMOGRAPHY AND MORTALITY ESTIMATION**

By

Cameron R. S. Thompson

B.S. State University of New York at Geneseo, 2007

A THESIS

Submitted in Partial Fulfillment of the  
Requirements for the Degree of  
Master of Science  
(in Marine Biology)

The Graduate School  
The University of Maine  
December, 2012

Advisory Committee:

Jeffrey Runge, Professor of Oceanography, Co-Advisor

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Thesis Co-Advisors: Dr. Teresa Johnson & Dr. Jeffrey Runge

An Abstract of the Thesis Presented  
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*Calanus finmarchicus* is a widely distributed copepod species that dominates the zooplankton community in the Gulf of Maine. It is of particular interest in its role as a major food source for the endangered northern right whale and stocks of herring, mackerel and cod. More accurate coupled models to predict its distribution requires better life history models. However, due to the difficulty in estimating it, mortality is often used as a closure term in those models; the value is justified mathematically rather than ecologically. Instantaneous mortality is difficult to measure, but the Vertical Life Table method (VLT) has gained some acceptance as an effective estimation technique. Calculations are made using the stage structure of the population and development rates. The VLT mortality estimations are heavily dependent upon development rates determined from temperature dependent functions and several assumptions. The limitations imposed by the VLT and inadvertent violations of assumptions prevented a spatial analysis of mortality. However, a new technique is presented to provide a much more explicit array of instantaneous mortalities that vary with season, stage and distance from shore. The Structured Population Molting rate method uses *in situ* incubations to directly observe the progressing stage structure and calculate the molting rates. The observed *C. finmarchicus* demography suggests that there is size selective

predation mortality corresponding with bathymetry. Near shore regions host various visual predators of late stage *C. finmarchicus* and lack a depth refuge through vertical migration. These factors could explain the paucity of later stages when compared to offshore regions, but an alternative hypothesis suggests that the Maine coastal currents are responsible for transporting *C. finmarchicus* to the deep off shore basins where they are found in great abundance.

## THESIS ACCEPTANCE STATEMENT

On behalf of the Graduate Committee for Cameron R. S. Thompson, I affirm that this manuscript is the final and accepted thesis. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine.

Signature: \_\_\_\_\_ Date: \_\_\_\_\_  
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## **ACKNOWLEDGMENTS**

This work has been supported with funds from the National Science Foundation.

The research presented here was part of a larger project, with many contributors. Along with Dr. Runge who was leading the research, I would like to acknowledge fellow graduate students Phoebe Jekielek, and Nick Record as well as lab manager Rebecca Jones and post doctoral fellow Frederic Maps. The Gulf of Maine Research Institute accommodated me while working in Portland, and Captains Robbie and Bryan of the R/V Ira C. and R/V Gulf Challenger, respectively, were a great help on the water. I would also like to thank my parents who helped me through the process of being a perpetual student.

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## Chapter 1

### POPULATION DYNAMICS OF *CALANUS FINMARCHICUS*

#### 1.1 Introduction

The planktonic copepod, *Calanus finmarchicus* is vastly abundant in waters of the northern North Atlantic Ocean (Heath and Lough 2007). *C. finmarchicus* is considered the most ecologically significant copepod in the North Atlantic (Melle et al., submitted), since it is both a dominant herbivore and an important food source for many species of economic concern (e.g. Dommasnes et al., 2000; Dalpadado et al., 2000; Darbyson et al., 2003; Smith and Link 2010). *C. finmarchicus* has been the focus of much research, leading to a wealth of knowledge on its biology with over 1000 research articles published since the publication of the classic book about the species (Marshall and Orr 1955), but there remain gaps in our understanding. One of the greatest challenges is the estimation of mortality rates, which are essential for understanding the control of the species population abundance and distribution (Ohman et al., 2004). Due to the difficulty in measuring mortality, it has often been parameterized by fitting the simulated results to observed data in math models (Runge et al., 2005). However, this tuning does not provide insight into the fundamental processes that drive mortality in *Calanus finmarchicus* population dynamics. Mortality is likely the result of predation, starvation and disease, but until reliable field rates are established hypotheses that explore such linkages will remain understudied.

In many regions of the northern North Atlantic and Arctic Oceans, *C. finmarchicus* has often been explicitly incorporated into ecosystem models while many other copepod species have received far less attention (deYoung et al., 2010). Due to the complexity of the ecosystem, a targeted species approach has been utilized to identify species for focused study. There are several criteria to consider in determining a species' relative importance including economic, ecological, and cultural significance. *Calanus*

*finmarchicus* has been chosen since its ecological role is pivotal to the trophic structure of the ecosystems it inhabits, and because its broad distribution enables comparative studies. However, the difficulties of oceanic research make even basic pieces of information hard to collect, and despite the success of the target species approach, the complete population dynamics of *Calanus finmarchicus* have yet to be described (Gifford et al., 2010). Many of the models featuring *C. finmarchicus* have, out of lack of understanding, simplified its complex life cycle, placing uncertainty into the model predictions (e.g. Pershing et al., 2009; Runge et al., 2010; Spiers et al., 2006; Carlotti and Radach 1996; Maps et al., 2010). This simplification of population dynamics has been advocated for in the rhomboid approach to modeling, in which the model resolution decreases with trophic distance from the species of concern (deYoung et al. 2004; 2010). Nevertheless, the growing recognition of managers' requirement for ecosystem forecasts which incorporate environmental changes highlights the need for greater comprehension of *C. finmarchicus* population dynamics (NMFS 2009). It has been the stated goal of oceanographic programs such as GLOBEC to form model predictions, but greater information is required before such an achievement is realized. Continued observation and data assimilation will be necessary for the improvement of population parameter estimates and models (deYoung et al. 2010).

Studying zooplankton has often played an ancillary role to investigating fisheries and oceanography, but its significance to ecosystems is paramount. Classically the role of zooplankton has been characterized by its capacity to transfer energy from primary producers to higher trophic levels (Miller 2004) However, the means by which energy is transferred through the food web to the species people eat is more complicated than typically depicted (Sundby 2000). Nevertheless understanding the population dynamics of zooplankton remains an essential task for forecasting the distribution and abundance of species which form vital links in marine food webs. Ubiquitous among these are the planktonic copepods, the prototypical intermediary link in coupled box-models (Miller

2004, Carlotti et al. 2000). Copepods are arguably the most numerous multicellular organisms on the planet (Schminke 2007), and unlike some of their planktonic neighbors, they are far more easily sampled and identified (Sameoto et al., 2000). Regardless, fisheries research has for the most part overlooked zooplankton, taking it for granted as part of an inherent carrying capacity of the ecosystem that often remains static in stock assessments (Castonguay 2008). The growing realization that a changing climate will alter basic ecosystem relationships has re-emphasized the importance of understanding processes above statistical relationships (NMFS 2009). Empowered by a mechanistic ecosystem understanding that includes the population dynamics of key copepod species, scientists will have a greater ability to make forecast to inform management decisions. Arriving to this point requires field estimates of mortality, for the parameterizing of models (Runge et al., 2005; deYoung et al., 2010; Gifford et al., 2010; Harris et al., 2010) and for understanding the relationship between survivorship and other life history characteristics (e.g. Ohman et al 2002).

### **1.1.1 Modeling Copepods in Marine Ecosystems**

The advancement of quantitative modeling approaches and the barriers to their improvement are well recognized. Application of models to ocean systems is now more feasible due to the convergence of new ocean observation technology, progress in physical oceanographic modeling, increased computing power, and greater data availability. These advancements have been utilized in oceanographic modeling especially with an emphasis on the physical attributes of the ocean and the resulting primary productivity (deYoung et al., 2010). The need to understand the biological interactions that influence primary production have been addressed through nitrogen-phytoplankton-zooplankton (NPZ) box models. These models typically use nitrogen, which is often converted from chlorophyll a concentration, to serve as the currency for the transfer of energy up through

the trophic levels. Such models focus on ‘bottom up’ factors that drive primary productivity while ‘top down’ controls, including mortality, remain a black box in which rates are determined mathematically rather than experimentally (Runge et al., 2005). One of the challenges of extending models up the food web is how to handle the complexity inherent with longer lived organisms (deYoung et al., 2010). Variability in physiology and behavior among different species and life stages within species determines biotic and abiotic interactions and consequently the abundance and distribution of a species. Models that compared copepod species have demonstrated the importance of differing life histories to their resulting populations (Ji et al., 2009). It has been further suggested by modeling work that relatively small tradeoffs in physiological rates contribute to the observed diversity of species (Maps, et al. 2012). The realization that differences in zooplankton life histories and selective feeding by predators has consequences for the ecosystem has helped motivate the development of several new modeling approaches (Travers et al., 2007; Runge et al. 2004).

Coupled biological-physical models have gained recognition as a means of taking advantage of the recent scientific advancements and combating the complexity of ecosystems (deYoung et al., 2010). Through this approach the physical properties of the ocean, including circulation and temperature, are accounted for and linked to life cycle models of various species up through a food web (Runge et al., 2005; Travers et al., 2007; deYoung et al., 2004). Describing the population dynamics of every interacting species in a system is not presently feasible; instead key species or functional groups should be identified (Fogarty and Powell 2002). In the Gulf of Maine, and in much of the northern North Atlantic, the copepod *Calanus finmarchicus* is one of these key species (Conover 1988). It has been suggested that we strive for end-to-end models, following the interactions through an entire ecosystem (Travers et al. 2007). These models would represent the entire food web and each species interaction with respect to the physical environment. The approach would necessitate multiple scales and two

way interaction between trophic levels (Travers et al. 2007). While end-to-end models may be an admirable goal, a more focused strategy has been proposed by deYoung and others (2004) which recognizes the uncertainties inherent in models. Generally we have more data on higher trophic level organisms because they have been easier to handle, observe, and study; we have far less data on zooplankton and species which are not economically important. The information is not available to completely parameterize a model of the ecosystem, instead it should simplify the interactions between species. The target species should have the greatest model resolution, while those above and below it are simplified (deYoung et al., 2004). According to Travers et al. (2007), such an approach is not true coupling since each level of the simulation is run separately and interactions only exist in one direction. Regardless, models that incorporate copepod life cycles differ substantially from the statistical approaches that are presently used in management (Babcock Hollowed et al., 2009).

Although stock assessment approaches that utilize statistical relationships among variables are useful, they are unable to account for uncertainty in our understanding of the system. Forecasts made from statistical models using available environmental indicators may perform poorly if the environmental conditions and response of organisms to it change (Drinkwater and Myers 1987). When the system changes the uncertainty manifests itself and the correlation deteriorates, which can have dire consequences. Understanding of causal links between environmental variables and species abundance is needed (Drinkwater 2005, Babcock and Hollowed 2009). An example of breakdown in statistical relationships in the zooplankton is the correlation between the North Atlantic Oscillation (NAO) and *Calanus finmarchicus* abundance (Planque and Reid 1998).

The correlation between *Calanus finmarchicus* abundance in the North Sea and Northwest Atlantic to the NAO index has long been recognized. The NAO index describes the alteration in pressure differences of air masses centered over the



Azores and Iceland, which determines the pattern of wind circulation and temperature (Fromentin and Planque 1996). When Fromentin and Planque (1996) realized that the index correlated with a shift in abundance of *C. finmarchicus* it was hypothesized that the population was influenced by the NAO's effect on primary production. However, Heath et al. (1999) offered a more nuanced explanation to the mechanisms controlling the correlation. They demonstrated that transport of overwintering *C. finmarchicus* from the Norwegian Sea to the North Atlantic and North Sea was primarily responsible for the population abundance. The correlation between the NAO and *Calanus finmarchicus* production exemplifies how bottom up processes transmit through the trophic structure to impact economically important species. The eventual breakdown of the correlation also emphasizes the importance of climate change and need for improved understanding of mechanisms controlling such relationships (deYoung et al. 2004). Bailey et al. (2000) managed to account for both by demonstrating how recruitment success of the commercially harvested walleye pollock shifted after a climate and ecosystem change. Recruitment was primarily controlled by mortality in the larval stages, but a climatic change instigated a regime shift in the community. After the ecosystem changed, mortality in the juvenile stage became more important to recruitment success. It is hypothesized that as part of the regime shift certain predators of the juvenile pollock became more abundant, and their survival rates diminished (Bailey et al. 2000).

### **1.1.2 Accounting for Climate Change**

There can be serious consequences when an ecological relationship is disrupted by climate change, especially when the observed correlation informs management decisions. The regime shift witnessed in the Gulf of Maine (GOM) between the 1980s and 1990s exemplifies the inability of stock assessments to account for uncertainty in its model of the ecosystem. It is hypothesized that a climatic change in the Arctic caused

cold, fresh water to travel down through the Labrador Strait, affecting the stratification of the water column and primary productivity in the GOM (Greene and Pershing 2007). Subsequently, the zooplankton community experienced an increase in small copepods over larger lipid rich *Calanus finmarchicus* (Pershing et al., 2005). During this time, fisheries management regulated to the best of their ability using biological reference points to encourage maximum sustainable yield (MSY). Despite measures to reduce fishing effort, some groundfish populations, including Atlantic cod, continued to decline and stocks have yet to recover (Fogarty and Murawski 1998; Mountian and Kane 2010). It's possible that the cumulative impacts of bottom up forcing and fishing pressure resulted in a regime shift consisting of changes in species composition and biological status, with more small sized individuals (Mills, 2010). Similar episodes may have played out with salmon responding to the Pacific decadal oscillation in the North West (Peterson and Schwing 2003), and cod responding to the NAO in the Canadian Maritimes (Drinkwater, 2002) and in the North Sea (Beaugrand and Kirby 2010).

The influence of the environment on the survival of larval fish has long been embodied in hypotheses to explain recruitment variability. The match-mismatch hypothesis that evolved from Hjort's (1914) early work recognizes the dependence of recruitment and year class strength on the larval stage (Cushing 1990). Inherent in the hypotheses stemming from this lineage is the importance of zooplankton as mediators of environmental influence (deYoung et al., 2010; Anderson 1988; Cushing and Horwood 1994). Despite the long standing recruitment problem ecologists continue to face the challenge of observational limits; although significant relationships may be detected between recruitment and an environmental variable, its influence is not quantified (Myers 1997). Myers (1998) notes that most of the relationships observed between temperature and recruitment occur in populations at the edge of their natural range, and these correlations are not often repeatable. In regards to the link between *C. finmarchicus* abundance and cod recruitment success, Myers (1997) concludes that there

may be a link between the two, but it is not strong enough to suggest the climate change will act through *C. finmarchicus* to affect cod. These criticisms highlight the need to understand the mechanisms underlining the statistically significant relationships and how they are driving the system. Once these goals are achieved coupled bio-physical models can be more robust and useful for understanding and predicting ecosystem responses.

It is increasingly realized that ocean basin ecosystem variability follows patterns on interannual, decadal and multi-decadal time scales. Although our knowledge of these patterns has expanded, predictions based on historical relationships should not be taken for granted, since they may fail for unknown reasons (deYong et al. 2004). The Intergovernmental Panel on Climate Change concludes that the warming of the planet and associated climate change will certainly have impacts on ocean ecosystems and their species (Parry et al. 2007). How these changes will affect the ecosystem is unknown, but politicians, fisheries managers and the public are nevertheless demanding predictions from scientists. Along with the increase in temperature, climate change will result in changes to ocean hydrographic properties, vertical stratification and circulation patterns. The response of species will depend on the conditions of each stock, but it is broadly recognized that cod distribution is moving northward (Drinkwater 2005), along with *Calanus finmarchicus* (Reygondeau and Beaugrand 2011). Thus, climate change is another reason why coupled physical-biological models should be used in making forecasts, and a reason why copepod life histories need to be parameterized.

Recognizing the ecological importance of *Calanus finmarchicus*, several workers have begun incorporating them into coupled models as a prey species driving the population dynamics of higher trophic levels. The endangered northern right whale is a highly migratory species, that can often be found following dense concentrations of its food source, *Calanus finmarchicus*. Greene and Pershing (2004) demonstrated that the whale's survival was sensitive to availability of *C. finmarchicus*, suggesting that a

climate driven reduction in their prey abundance contributed to lower reproductive rates. Following that work Pershing and others (2009) simulated the interannual abundance of *C. finmarchicus* using readily available data coupled to a model of the copepods life cycle. They could forecast when the whales would be present in their feeding grounds (Pershing et al. 2009). This information can be utilized by managers to prevent ship strikes and fishing gear entanglements. A similar linked coupled model strategy was proposed for predicting the environmental influences on recruitment success of cod (Runge et al., 2010). Considering the importance of *C. finmarchicus* to the diet of mackerel and herring (Prokopchuk and Sentyabov 2006; Darbyson et al., 2003; Castonguay 2008), the same approach should be utilized for these species. In discussing the creation of coupled models, the lack of mortality estimates is often cited as a hindrance to future advances (e.g. Melle et al., Submitted; Neuheimer et al., 2009; Rune et al. 2005). The studies of mortality are rare, and there is far more information on the other aspects of *C. finmarchicus* life history.

## **1.2 *Calanus finmarchicus* Life History**

### **1.2.1 Life Cycle**

After hatching, an individual *Calanus finmarchicus* copepod must pass through 6 nauplius stages (NI-NVI), the first two of which are non-feeding. It then undergoes a metamorphosis to its copepodite body form, developing through 5 more stages (CI-CV), finally reaching adulthood (CVI) as a male or female (Melle et al. submitted). Its development through the life cycle is dependent on the temperature and availability of food, with the time between stages increasing with colder water and less food (Campbell et al., 2001). During the pre-adult (CV) stage *C. finmarchicus* can undergo diapause, characterized by residence in deep water, arrested development, reduced metabolism, and torpor. The behavior, which is found in some calanoid species, is a life history

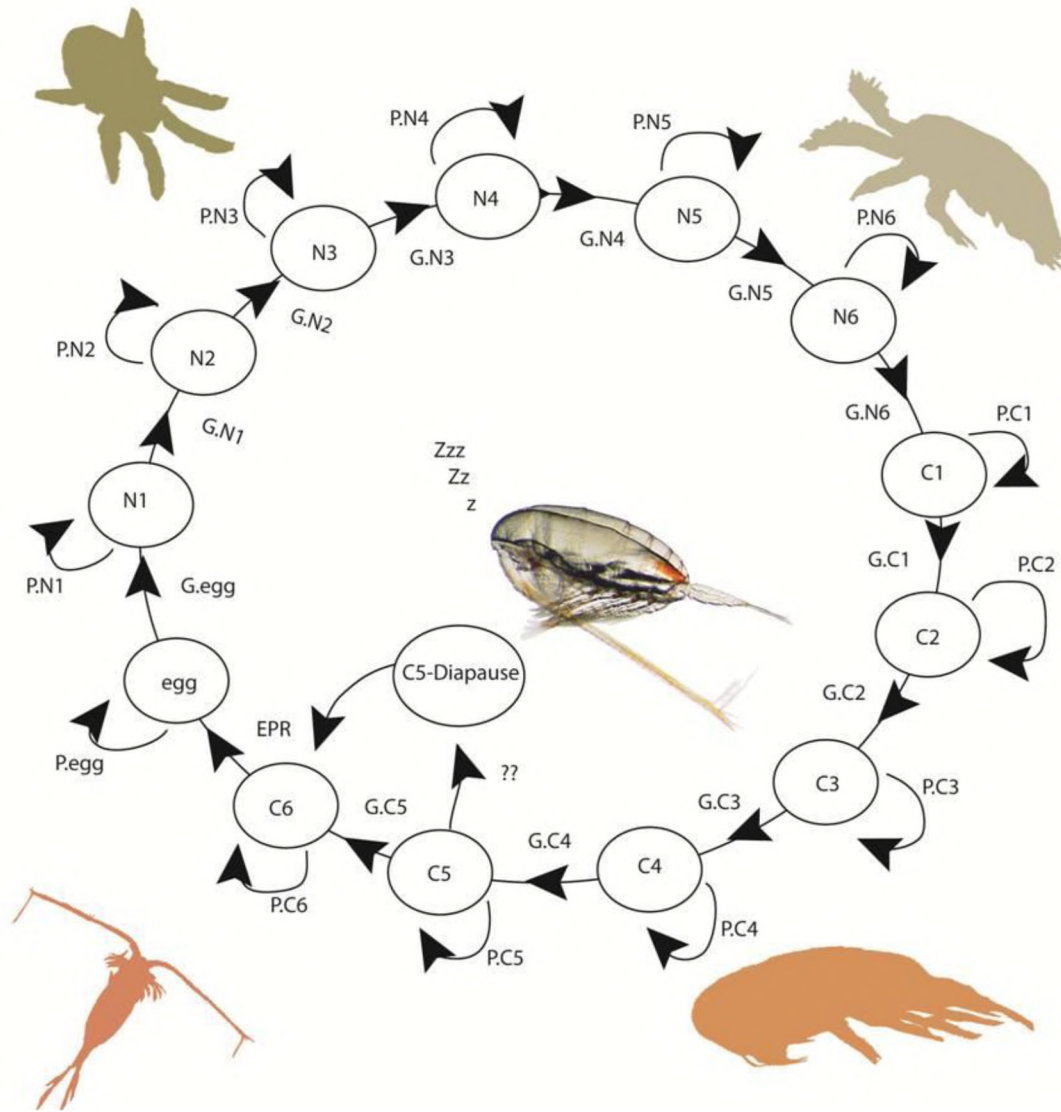


Figure 1.1. Life Cycle. The 13 developmental stages of *Calanus finmarchicus*, along with the possible diapause stage. Individuals mature through an egg stage, 6 nauplius stages (N1 - N6), 5 copepodite stages (C1-C5) and a final adult stage (C6) at which point females produce eggs (EPR). G, represents the probability that the individual will grow and develop into the next stage while P is the probability it will remain in its current stage.

adaptation to unfavorable conditions (Hirche 1996). Diapause favors survival during times of low food availability or high potential for mortality (Dahms 1995, Ohman 1988, Stearns 1992).

Along with mortality, understanding diapause remains one of the great challenges for modeling copepod life cycles (Runge et al. 2005). Several attempts have been made to find significant relationships between environmental signals and the timing of diapause, yet the variability in timing across its range is not consistent with response to any single environmental cue (Johnson et al., 2008). Models of *Calanus finmarchicus* life cycles have relied on various methods to match diapause timing to observations, such as specifying an entering fraction and duration for diapause (e.g. Speirs et al., 2006). However, the duration is also variable; for example the median for the eastern North Atlantic is estimated to be 270 days, compared to 200 days in the western North Atlantic (Melle et al. submitted). An alternative hypothesis, the Lipid Accumulation Window, proposes that pre-adult *C. finmarchicus* enter diapause once they've acquired a necessary minimum amount of lipids. These lipids sustain the individual through the overwintering period and provide the energy necessary for the final adult molt and gonadal maturation. While diapause metabolism is reduced, it does not cease, and individuals gradually use up their lipid stores, emerging when a certain amount remains. This hypothesis is capable of accounting for differing durations since the rate of metabolism is dependent on water temperature (Saumweber and Durbin 2006). Thus, in the Gulf of Maine where deep water is relatively warm, *C. finmarchicus* emerge after a much shorter duration than typically found. As temperatures rise in these waters, the survival of the resident population may be challenged (Maps et al., 2012).

The deep waters of the ocean basins are cooler than the shallower water in Gulf of Maine and may provide a more hospitable habitat by promoting longer diapause duration. However, the primary productivity is generally less in the basins than on the shelves, resulting in lower production rates of *C. finmarchicus* eggs (Melle et al.

submitted). It has been well documented that the number of eggs produced is hyperbolically related to the food availability (Melle et al. submitted). Thus, the life cycle of *C. finmarchicus* along with the seasonality of ocean production and temperature dictates the interannual population pattern. Typically adults will emerge in winter and the next generation will begin to emerge in early spring with the abundance being greatest prior to the warm summer season. During summer and fall the late pre-adult stage enters diapause, leaving the upper water column. Due to the variability of the productivity and environment, different regions across their natural range will feature unique annual cycles. Furthermore, many of the *C. finmarchicus* populations are characterized by a multi-annual life cycle, with some regions hosting up to three generations, but the actual number depends on local conditions (Melle et al. submitted).

Mortality, another key driver of population dynamics, is also dictated by local conditions. However, unlike many of the previous parameters, mortality is not easily discerned from field measurements or laboratory studies (Harris et al., 2010). Higher mortality rates have been linked to higher temperatures, but this is likely an inadequate proxy for the predator field (Speirs et al., 2006; Gentleman et al., 2012). Acquiring a greater understanding of *C. finmarchicus* life history necessitates the estimation of mortality in the field. Once the spatial and temporal pattern is better described and the relationship with other factors more understood, a robust model of survivorship can be developed.

### **1.2.2 Mortality and Life History**

According to life history theory, species will develop strategies that maximize their fitness, but because of physical and biological constraints they must make trade-offs among traits. The evolution of these traits determines the population dynamics of interacting species and the theory can be used to understand the broad features of a lifecycle. When considering the principal traits and the tradeoffs between them the

currency of relative fitness is often measured with survivorship or potential mortality (Stearns 1992). Thus, mortality is key to understanding the life history and population dynamics of an organism. Mortality may be the result of starvation, non-hatching, sinking eggs, egg cannibalism, and disease among several other possible sources, but the principal cause is predation (Gentleman et al., 2012; Tsuda, 1994; Tang et al., 1998; Heath et al. 2008). The importance of predation to zooplankton population dynamics has long been recognized, and the behaviors employed by the prey to lower the risk have been documented (e.g. Frost 1988; Bollens and Frost 1991). Acting at different points along the predation sequence, prey behavior can lower the probability and success of an encounter with a predator through avoidance, escape, and defensive means (Ohman 1988). Furthermore, Verity and Smetacek (1996) argue that “...predation and resource availability act through morphologies and life history strategies of organisms to structure pelagic ecosystems...” Resulting from strong natural selection, with predation being a chief component, copepods have evolved a limited morphological diversity and only a few species dominate the water column, especially in northern latitudes. The avenue through which many species have adapted is their life cycle (Verity and Smetacek 1996; Kiorboe 2008).

A comparison between two copepod species, *Calanus finmarchicus* and *Pseudocalanus spp.*, demonstrates the life history tradeoffs that can evolve among two co-occurring species. While *C. finmarchicus* is a relatively large-bodied copepod that produces numerous eggs through broadcast spawning, *Pseudocalanus spp.* is a small-bodied egg brooder. The brooding behavior enables the copepod to protect the eggs until they hatch, but it restricts the number produced. The tradeoffs between these strategies are illustrated in the stage specific mortalities of the two species, with *Pseudocalanus spp.* having a more uniform mortality regime compared to *C. finmarchicus*. *C. finmarchicus* experiences high mortality in its egg and non-feeding nauplius stages, which may be due to cannibalism (Ohman et al., 2002). Adult *Calanus* emerging from



dormancy begin to reproduce, but there might not be enough food in the water for the population to grow. Ohman and Hirche (2001) have found that there is a pattern of density dependent mortality for eggs at this time, which they suggest is due to cannibalism, a conclusion corroborated by other studies (Ohman 2008). According to Kaartvedt (2000) the early emergence of adults prior to the bloom enables their offspring to take advantage of the plentiful food during the peak. Predation by planktivorous fish is an important driver of the life history. The new generation of *C. finmarchicus* are able to develop through their life cycle and enter dormancy prior to the high predation risk of summer time. When diapausing they migrate below the depths commonly occupied by their visual predators (Kaartvedt 2000).

Diapause is a feature of species in the genus *Calanus*, but is not found among all copepods. However, diel vertical migration (DVM) is found the world over in a wide range of marine and freshwater zooplankton taxa, and like diapause, it typically involves migration to depth. Typically organisms will inhabit the surface layer at night and migrate to depth during the day. There is a clear energetic and opportunity cost to DVM and according to life history theory there must be some benefit (Stearns 1992). The most widely accepted reason is its role in reducing the risk to visual predators, with the mantra being ‘better hungry than dead’ (Hays 2003). The predator field affects the mortality rate and visual predators such as fish are particularly voracious. Thus, these two behaviors, diapause and DVM, are both driven by the adaptive advantage of avoiding visual predators (Bagoien and Kaartvedt 2001). Many studies of *C. finmarchicus* mortality have indicated that there are stage specific differences as well as temporal and spatial variability (e.g. Ohman et al. 2004; Bagoien et al. 2001; Eiane and Ohman 2004; Hirst et al., 2007; Ohman and Hsieh 2008; Plourde et al., 2009). The results of such mortality studies have significant implications for our understanding of *C. finmarchicus* life history, population dynamics, and observed demography.

### 1.3 Mortality Estimation

Regardless of the reasons behind the differences in mortality regimes among regions and stages, they have to be supported by measurements of mortality. Estimating *in situ* mortality is a difficult task, but procedures have been developed. Mortality estimation techniques follow the lines of a few principal methods; below, I highlight the vertical and horizontal approaches. Each has its own particular advantages and accompanying assumptions. As arthropods, copepods have the convenient characteristic of developing through several morphologically distinct life stages, allowing the observation of population structure. Among all methods mentioned here this information plays a crucial role in calculating population parameters, whether it utilizes life history theory (Myer and Runge 1983), tracks a cohort over time (i.e. horizontally) (Aksnes 1997, Landry 1978) or examines the population structure at a single point in time (i. e. vertically) (Aksnes and Ohman 1996).

With the horizontal method, and the cohort approach more generally, the zooplankton population of interest is tracked over time through repeated sampling. This requires that a clearly distinct cohort can be identified in the population and that this population be continual sampled throughout its development (Aksnes 1997). The approach assumes no advective immigration or emigration of stages into and out of the population. Such a violation would negate the ability to attribute population changes to a common development and mortality regime. Thus, the horizontal method is restricted to conditions in which advection would be limited. Successful application has been documented in Norwegian fjords (Eiane and Ohman 2004), isolated bays (Landry 1983) and within enclosed water masses (Ohman et al., 2002). However, broad use of the cohort approach is hindered by the pelagic nature of the target populations and prohibitive costs of repeated sampling. Where the horizontal method falls short the vertical life table method gains merit through its relaxation of the no advection requirement.

The vertical life table (VLT) method was promoted by Aksnes and Ohman as a way of measuring mortality without the necessity of a long time series of enclosed populations (1996). A common problem in the marine realm when doing repeated sampling is the difficulty of discerning whether differences in abundance over time are due to population dynamics or advection. It may be that the population sampled had come from an upstream source and the current measurements have no connection to the previous ones. In the VLT method the concerns over advection are relaxed and time series becomes unnecessary. According to the vertical approach, the stage structure represents the cumulative experiences of the population including mortality. The relative differences between stages is from recruitment out of the previous stage and into the subsequent one. Therefore the only parameters necessary for estimating mortality are stage structure and development time, the difference between what is expected and what is observed must be accounted for by mortality. This is the basis of the VLT, the details of which are explored by Aksnes (1997) and Gentleman et al. (2012); we further review the method in Chapter 3 of this thesis. The next chapter utilizes the VLT to examine spatial and temporal variability in the Gulf of Maine. Along with an examination of mortality, we will describe the abundance and demographic patterns, which with the literature review presented here, give further insight into the population dynamics of *Calanus finmarchicus*.

## Chapter 2

### DEMOGRAPHY OF *CALANUS FINMARCHICUS*

#### 2.1 Introduction

*Calanus finmarchicus* is a ubiquitous marine copepod in the northern North Atlantic. It plays an ecologically significant role in the Gulf of Maine, where it resides at the southern end of its range. Its dominance of zooplankton biomass in the Gulf of Maine is well documented, and it is a primary source of food to species of concern such as right whales and herring. Although *C. finmarchicus* has received much attention, many of the processes governing its population abundance and distribution remain understudied. Mortality rates in copepod populations are difficult to study since they cannot be observed *in situ*, yet this process plays a vital role in population dynamics. Copepod demographic data represent the integration of factors affecting their population dynamics and provide a wealth of information from which the processes might be inferred. The Vertical Life Table method (VLT) is a technique that utilizes the demographic data to calculate mortality. Here, I contribute to the knowledge of *C. finmarchicus* demography in the Gulf of Maine during the late summer and spring. I describe its distribution and abundance and analyze mortality through the VLT method. I find support for two possible explanations for the differential stage structures exhibited by the nearshore coastal and offshore components of the population. I hypothesize that distinct predator assemblages in these two areas exert selective predation pressures, with the visual predators targeting older copepods in nearshore waters. Circulation patterns in the Gulf of Maine may also affect *Calanus finmarchicus* coastal demographic through advection. It is likely that both forces are important factors for determining the observed demography.

### 2.1.1 Studying Zooplankton

Biological oceanography and especially the study of zooplankton must contend with the challenge of describing processes on multiple scales through information provided by discrete samples. The past few decades have witnessed great technological advancement in the methodology employed to sample the ocean, but traditional net tows continue to be irreplaceable. Satellite imaging, station buoys, and drifters are capable of continuously providing data about the physical characteristics of the water which can later be used for modeling productivity. Acoustic and optical devices that are now available help describe the zooplankton community by providing information on their relative abundance, size frequency, and distribution. However, these advances are unable to accurately discern the biomass or composition of the community (Harris et al. 2000).

Ship-deployed instruments such as the plankton net have been in use for over a century and continue to provide valuable data. Variations and improvements have been made with pumps capable of collecting discrete volumes of water and nets which open and close at specific depths (Harris et al. 2000). Nevertheless, scientists are continuously confronted with the issue of sampling accuracy; how representative of the zooplankton community is the sample? Through the accumulated knowledge of many research cruises and sampling tows, the biogeography and phenology of the ocean ecosystem is better described and understood. These abundance and distribution patterns are influenced by both abiotic and ecological factors. In the case of copepod biology it is likely that mortality via predation is a key driver of population dynamics. It has already been demonstrated that *Calanus finmarchicus* mortality varies between different regions (Ohman et al. 2004). Furthermore, the zooplankton community can be variable within the Gulf of Maine with larger species inhabiting the offshore waters compared to the coastal zone (Frank 1988). Here, I contend that predation and its influence on mortality depends upon the season and bathymetry within the Gulf of Maine. Shallow nearshore

waters that are relatively warm and well mixed in the summer are certainly different than the deep basins, and in this chapter I attempt to demonstrate that these differences influence *C. finmarchicus* populations.

### **2.1.2 Sampling Considerations for Estimation of Mortality**

Another challenge to describing the oceanic plankton is determining how many samples are needed to accurately represent the community in the spatial and temporal domain of concern. At one time it was assumed that phytoplankton were homogeneously distributed throughout the water column, we now understand that nested patchiness is a common feature of zooplankton (Pinel-Alloul 1995). As early as the 19th century the assumption of homogeneity has been challenged, but patchiness wasn't well documented until the 1960s (Pinel-Alloul 1995). Although not well understood, early workers such as Barnes and Marshall (1951) showed that the distribution was non-random, describing their observations as 'swarms.'

Patchiness is the result of biological and physical processes acting at different scales and the scale to be examined depends on the process under investigation. It has been argued that physical processes such as ocean circulation are far more influential on the larger scales, while ecological factors drive small scale patchiness (Pinel-Alloul 1995). However, some (Folt and Burns 1999) have suggested that biological processes such as diel vertical migration, predator avoidance, locating food patches and finding mates, are far more influential than previously realized. Diel vertical migration influences large scale forces such as advection. Since advection is depth-dependent its effect on the community is determined by the vertical distribution of its members. Predators can directly remove animals from a population and elicit behaviors in potential prey that reduce local concentrations. The locating of food patches and mates both cause aggregations of zooplankton (Folt and Burns 1999). The forces behind patchiness act

in a complex manner to result in the observed distribution of zooplankton (Pinel-Alloul 1995).

The study of spatial heterogeneity has typically been more concerned with abundance rather than composition of the zooplankton community. Early investigations discovered a high degree of variability in samples for abundance, depending on the concentration of the organism (Winsor and Clarke 1940). The temporal and spatial scale of sampling are also important factors affecting the variability, which increases with the distance between samples (Pinel-Alloul 1995). It was also recognized early on that abundance and composition exhibited different patterns of variability. While the abundance of an organism may differ significantly between replicates, the proportion may not. As Winsor and Clarke put it, there is a "...tendency for the numbers in any haul to be high or low together..." (1940, 4) . However, these patterns are species specific (Barnes and Marshall 1951), which may be influenced by the size, since heterogeneity decreases with larger organisms (Pinel-Alloul 1995). Furthermore it has been demonstrated that replicates taken right after each other are not significantly different, but eventually become so as time between tows increases (Winsor and Clarke 1940, Barnes and Marshall 1951). These are all issues to be considered when designing sampling protocols.

In their description of the vertical life table method for mortality estimation, Aksnes and Ohman (1996) were particularly concerned with variability due to patchiness. Their recommendation was to combat the variability through repeated sampling. We follow that recommendation and employ the VLT approach for calculating mortality. Unfortunately, several challenges arose when utilizing the VLT method for analysis of cross shelf mortality. Regardless, the data presented provides valuable information on the demography of *Calanus finmarchicus* in the Gulf of Maine.

## **2.2 Processes Influencing *Calanus finmarchicus* Demography**

### **2.2.1 Gulf of Maine Bathymetry**

The northwest Atlantic is characterized by large shelves harboring rich fisheries supported by high lower trophic level productivity of the region. The Gulf of Maine is a semi-enclosed sea stretching from Nova Scotia to Cape Cod, bounded by Georges and Brown Banks and connected to deeper northwest Atlantic shelf waters by the Northeast Channel. Much of the primary production results from the nutrient rich waters supplemented by mixing with deep shelf waters and input from many estuary systems. Following the winter mixing a vital and large spring bloom occurs, after which strong vertical stratification hinders further production in deep waters of the Gulf. Properties of the water are affected by both eddies from the Gulf Stream and cyclonic storms from the south, but the greatest influence stems from upstream waters in the north (Townsend et al. 2004; Pettigrew et al. 2005).

The Labrador Subarctic Slope Water is a cold and relatively fresh water mass that can flow south and pass over the Scotian Shelf to enter the Gulf of Maine through the Northeast Channel. More commonly, this deepwater entrance into the Gulf of Maine connects the Scotia Shelf Water to the three deep basins: Georges, Jordan and Wilkinson. A general counter-clockwise circulation is evident in the Gulf of Maine with cyclonic eddies featured in the basins (Townsend et al. 2004; Pettigrew et al. 2005). The general circulation is driven by water masses of contrasting densities from the deep slope, and surface water fed by river discharge along with influx from the Scotia Shelf (Townsend et al. 2004). The Gulf of Maine is considered to be highly productive, driven by some of the largest tidal ranges in the world. The tidal forces are strongest in the east where the water column is well mixed and surface water remains relatively cold throughout the summer. The buoyancy driven Eastern Maine Coastal Current (EMCC) extends into the central Gulf of Maine while the Western Maine Coastal Current (WMCC)



stretches from the midcoast to Cape Cod, generally following the 100 meter isobath. Along with the influx of nutrient rich slope water the tidal mixing is vital for regenerating nutrients, and enables sustained production beyond the spring bloom (Townsend et al. 2004).

The Maine Coastal Current significantly influences the physical properties of water masses in the Gulf of Maine, and it is a defining characteristic of the inner shelf region (depths < 100 m) (Pettigrew et al. 2005). It is typically considered as the EMCC and WMCC with the former featuring greater velocities. Driven by tidal forces the EMCC flows out from the Bay of Fundy along the coast towards Penobscot Bay, at which point the core of it veers south into the Gulf of Maine (Pettigrew et al. 2005). This dense core of the EMCC may subduct beneath the surface waters of the cyclonic basins. Some of EMCC contributes to the WMCC, but there is a great deal of variability inter-annually, as well as seasonally. The WMCC headwaters have been identified as within the Penobscot Bay and its water properties are generally warmer with lower salinity, and density. As it flows along the coast, the discharge of river systems contributes to the surface waters of the current, causing sequential freshening and displacement of the water mass (Pettigrew et al. 2005).

The inner shelf surface flow is dominated by this river discharge, but occasional deep water currents extend into the western Gulf. The WMCC is further characterized by partially wind driven plumes of water extending out from the coast and contributing to the properties of surface water in the western Gulf including Wilkinson Basin. Several water masses can be identified due to the influence of the coastal current, these significantly affect the demography of *C. finmarchicus* presented in this study. Adjacent to Jordan Basin is the core EMCC, and there is an inner shelf portion which veers to the southwest to contribute to Wilkinson Basin. The WMCC impacts the greatest number of our study sites since it extends along the coastal inner shelf waters from Penobscot Bay to the surface waters of Wilkinson Basin (Pettigrew et al. 2005). The

velocity of the WMCC is depth dependent with the greatest speeds occurring near the surface (Churchill et al. 2005). Considering the stage specific depth profile of *Calanus finmarchicus* and temperature dependent development, these circulation patterns could impact their demography and distribution (Lynch et. al 1998).

### **2.2.2 Predation Mortality**

Mortality has a significant impact on the population demographics of copepod populations. Although there are numerous sources of mortality including starvation and disease, predation is the most important driver and most variable factor (Gentleman et al., 2012). *Calanus finmarchicus* is a ubiquitous species with numerous predators including seabirds (Brown and Gaskin 1988), whales (Baumgartner 2003), ichthyoplankton (Heath and Lough 2007), planktivorous fish (Kaartvedt 2000), invertebrates (Sullivan and Meise 1996), and other copepods (Sell et al. 2001). The selectivity of these predators on specific stages depends on the species, its ontogeny, and vertical distribution. Thus, it is expected that regions featuring distinct predator assemblages will differentially impact the local *C. finmarchicus* population. Studies of freshwater lakes have demonstrated how foraging behavior of predators controls copepod populations. Planktivorous fish preferentially consume the larger copepods and this size selection leads to the sequentially elimination of copepod stages and species (Langdon 1968). Here I suggest that the population demography of *Calanus finmarchicus* is dependent on mortality, and the different predator assemblages of the inner shelf and basins will be reflected by the demography data.

In an effort to simplify complex ecosystems in order to take advantage of improved modeling capacity, one approach is to identify and focus on the most important species (de Young 2004; Fogarty and Powell 2002; Gifford et al. 2010). The massive northern right whale famously uses its baleen plates for filtering copepods particularly *Calanus finmarchicus* for food. Despite their large size and appetite, the

scarcity of right whales implies that they do not exert significant mortality on copepod populations at a regional scale (Baumgartner 2003). The red necked phalarope is a similarly charismatic species that relies on *C. finmarchicus* for food (Brown and Gaskin 1988), but hasn't been considered as affecting population dynamic. In these instances *Calanus finmarchicus* is studied in the context of the predator's population dynamics, the same is often true for recruitment of commercially important fish ( e.g Beaugrand et al. 2003).

*C. finmarchicus* has been identified as a key prey species of larval gadids, particularly cod in the northeastern Atlantic, and there is also evidence that *C. finmarchicus* is an important prey of cod larvae in the Northwest Atlantic at certain times of year (e.g. Kane 2007). Spring spawning and settlement in nearshore nursery grounds enables these larvae to take advantage of the rapidly increasing population of copepods (Heath and Lough 2007). In their early developmental stages these larvae are equipped with large eyes, which makes them effective visual predators. Foraging is limited by the gap of their mouth, which means prey size increases as they grow. Larval fish may start feeding on copepod eggs and early stages of naupli, they then advance to later naupliar stages and eventually copepodites. This shift to copepodites necessitates an increase mobility of the larva in order to capture their prey. Eventually the larval fish grows and begins to feed on a wide range of macroplankton, including euphausiids (Heath and Lough 2007). As the fish mature they undergo ontogenetic shifts and move from their nearshore nursery habitats to deeper colder water. Depth and temperature are key habitat determinates of gadids, with the larger fish occupying deeper waters (Methratta and Link 2007), but at this point they are no longer voracious predators of copepods.

Planktivorous fish, such as herring and mackerel continue to be significant predators of copepods after the planktivores develop out of the larval stages. These pelagic fish undergo feeding migrations during which they target *Calanus finmarchicus*. It has been further suggested that the timing and location of these migration patterns has been

adapted to coincide with the spring bloom and subsequent increase in copepod populations (Kaartvedt 2000; Corten 2000). The Gulf of Maine nearshore waters are occupied by several species of forage fish during the spring including Atlantic herring, Atlantic mackerel, alewife, Atlantic menhaden and others (Jordaan et al., 2010). The significance of *Calanus finmarchicus* to mackerel and herring diets has been supported by analysis of stomach contents which also revealed a preference by herring for the larger, lipid-rich late copepodid stages (Darbyson et al., 2003; Prokopczuk and Sentyabov 2006). Thus, Kaartvedt (2000) argues that the life history of *C. finmarchicus* is driven by predation of planktivorous fish such as herring and mackerel. Their spawning occurring before the peak spring bloom enables offspring to take advantage of the abundant food supply and develop through life stages quickly. Once they reach the pre-adult CV stage they may enter diapause for the duration of the summer (Kaartvedt 2000).

Diapause and diel vertical migration are predator avoidance behaviors utilized by *Calanus spp.* to reduce encounter rates with predators (Ohman 1988). Both behaviors feature migration to depths below what is typically occupied by epipelagic planktivorous fish (Kaartvedt 2000, Hirsche 1996, Prokopczuk and Sentyabov 2006). Diel vertical migration typically involves the daily movement from shallow depths at night to deeper waters during the day (Hays 2003). Diapause is a life history strategy for avoiding unfavorable conditions, it features both a behavioral and physiological change that can last for 270 days or more in *C. finmarchicus* (Hirsche 1996, Melle et al. submitted). These strategies reduce mortality by physically separating copepods from predators and through reducing the efficacy of visual predation (Hays 2003, Hirsche 1996). The reduced visibility provided by depth and night time foraging lowers the chances of being detected by a predator, which becomes important for larger pigmented species (Hays 2003). Diapause of late stage *Calanus finmarchicus* takes this strategy further by occupying depths between 400 and 1000 meters on the outer shelves (Melle et al. submitted). Although there are reasons beyond predator avoidance for occupying those deep waters

it is a driving force of their life history (Hirche 1996). These behaviors rely on the reduced visibility provided by depth, but what happens when the bathymetry and water properties prevent migration to depth? *Calanus finmarchicus* is considered to be an offshore copepod species (Melle et al. submitted), but it nevertheless occupies the inner shelf waters in the Gulf of Maine shallower than approx. 100 m where it cannot reduce predation detection through these behaviors.

The relative importance of visual predation compared to other forms of predation is dependent upon local ecosystem factors, but nonetheless contributes significantly to mortality. In one study the impact of visual predators to copepod mortality has been shown to be much greater than non-visual predators, such as invertebrates that rely on tactile stimuli (Bagoien and Kaartvedt 2001). Contradicting those results, Eiane and others (2002) demonstrated through a similar study of two different fjords that invertebrates can contribute greatly to early stage mortality. One of the fjords lacked vertebrate predators and *C. finmarchicus* mortality was very high for the early stages and dropped for the later stages, it was suggested that the invertebrate predators consumed the smaller copepods, but could not prey on the larger ones. The other fjord was characterized by uniform mortality that while substantial, was less than that for early stages in the other fjord; here the visual vertebrate predators could consume all *C. finmarchicus* stages while simultaneously consuming the invertebrate predators (Eiane et al 2002). Another study carried out on Georges Bank found invertebrate predators and cannibalism to be a dominant sources of mortality for egg-N3 stage *C. finmarchicus*. It was suggested that abundant copepod predators and hydroids were responsible for much of the mortality (Ohman et al., 2008). Although typically found in the benthos hydroids can be suspended in the water column by storms and consume copepods at a rate which makes it competitive with larval cod (Concelman 2001). However, as gelatinous zooplankton, hydroids are difficult to sample and enumerate. The most common invertebrate predators on Georges bank are the chaetognaths *Sagitta elegans* followed by cnidarians,

euphausiids and amphipods. The invertebrate predators are primarily found in the shallow well mixed waters of Georges' Bank central shoal area, above the 100 meter isobath. Departing from that distribution, euphausiids are found in deeper waters and are particularly abundant in the spring beyond the 100 meter isobath of the inner shelf (Sullivan and Meise 1996). The survey, from which the previous distributions were found, did not sample the inner shelf waters in the Gulf of Maine. Nevertheless, the warm, shallow, well mixed water could host an assemblage of invertebrate predators similar to George's Bank and they may exert the same influence on *C. finmarchicus* population dynamics.

The adaptive advantage of visual-predator avoidance has significant implications when considering the distribution of *C. finmarchicus*. Many studies of *C. finmarchicus* mortality have indicated that there are stage specific differences as well as temporal and spatial variability (e.g. Ohman et al. 2005, Plourde et. al. 2009, Eiane et al. 2002). Nearshore regions that are shallow cannot provide the depth refuge from visual predation, and may also feature greater mortality from invertebrates. According to this hypothesis the inner shelf, (i.e. less than 100 meters in depth), is occupied by an abundance of visual predators including fish larvae and planktivorous fish. Due to selective feeding on the lipid rich copepod and increased visibility owing to their relatively large size, late stage *C. finmarchicus* are vulnerable to predation by visual predators. The shallow water hinders the predator avoidance behaviors of diel vertical migration and diapause, and it enables the proliferation of numerous invertebrate predators. The impact of invertebrate predators on the demography is unclear, but will likely decrease the overall abundance. Regardless, any population located in these regions should have a relatively lower abundance and a stage structure skewed towards younger copepodites which are smaller sized and less conspicuous. Using the observed demography and a calculation of instantaneous mortality the differences between the nearshore and offshore *Calanus finmarchicus* populations will be analyzed in order to evaluate my hypothesis.

## 2.3 Methods

### 2.3.1 Procedures

Sampling methods are based on the Atlantic Zone Monitoring Program (AZMP) protocols (Mitchell et al. 2002). A double ring net with diameters of 0.75 m and 200  $\mu\text{m}$  mesh was used to collect zooplankton samples. It was towed vertically from 5 meters off the bottom at a rate of 40 m/min. The volume of water filtered was calculated with the aid of a General Oceanics flowmeter suspended across the opening of each ring. The number of tows conducted at each sample site ranged from 4 to 10. At the surface the contents of the cod end were transferred to glass sample jars and preserved with 4% seawater-buffered formaldehyde solution. In the laboratory these jars were divided in half using a Folsom Plankton Splitter. Half of the sample would be preserved for identification and enumeration while the other half was processed for dry weight. Samples were separated from the formaldehyde preservative through mesh sieving and a 100mL freshwater rinse, afterwards they were dried in a Precision Econotherm oven at 65 °C for 48 hours. The weight of the dried samples would then be measured to the nearest 0.001 g with subtraction of the preweighted mesh and drying dish. If any debris or euphausiids were found in the sample they would be removed with the euphausiids weighed separately using the same technique. The archived half of the sample was diluted and subsampled using a Stempel Pipette, the volumes of which were recorded so that abundance could be calculated. Since this study was solely concerned with the late stage *Calanus finmarchicus*, development stages C1 to adult females and males were identified; other zooplankton in the catch were not enumerated. Subsampled were enumerated with a target of 200 *Calanus finmarchicus* individuals to be identified, but the number would increase to 400 in order to enumerate at least 5 copepods in each stage.

The Vertical Life Table (VLT) method utilizes the population structure and development times of *Calanus finmarchicus* to estimate instantaneous mortality (Aksnes and Ohman 1996). Analysis of the replicate zooplankton samples provides demographic information on the *Calanus* population, including its stage structure. Development times are calculated from the water temperature using a Belehradek temperature function provided by Campbell et al. (2001). At each station a SeaBird 19 Plus was deployed to obtain a conductivity, temperature, and depth (CTD) profile of the water column from 5 meters off the bottom to the surface. Temperature from these profiles was averaged for the top 40 meters and used in the Belehradek temperature dependent development function for *Calanus finmarchicus* (Campbell et al. 2001) (Eq 2.1). Mortality estimates for joint stages CI to CVI are calculated from the replicate samples using the VLT calculation and averaged at each sample site (Aksnes and Ohman 1996) (Eq 2.2). A multifactor analysis of variance was then performed to investigate the relationship of instantaneous mortality with season and bathymetry.

$$DT = a(T - \alpha)^b \quad (2.1)$$

Equation 2.1 Belehradek temperature function using parameter values derived from Campbell's (2001) study on *Calanus finmarchicus*. Inputting a °C temperature into  $T$  will estimate  $DT$ : the development time in days from the midpoint of the egg laying period to the time when 50% of the copepods have reach that stage. While  $\alpha$  has been found to be -9.11 and  $b$  is equal to -2.05, the value of the  $a$  parameter depends on the stage of interest (Campbell et al. 2001).

$$\frac{e^{m_i DT_{i-1}}}{1 - e^{-m_i DT_{i+1}}} = \frac{N_i}{N_{i+1}} \quad (2.2)$$

$$m_{C5-C6} = \frac{\ln[N_{C5}/N_{C6} + 1]}{DT_{C5}} \quad (2.3)$$



Equation 2.2 & 2.3: Vertical Life Table method estimation of instantaneous mortality for joint stages (Aksnes and Ohman 1996). The first equation 2.2 applies to juvenile stages (C1-C5) and the 2nd (2.3 is for the pre-adult and adult stage (C5/C6).  $i$  is the stage,  $m$  ( $day^{-1}$ ) is instantaneous mortality,  $D$  is the development time in days, and  $N$  is the stage abundance, which becomes unitless. A full description of the VLT equation and its derivation can be found in chapter 3 of this thesis (3.2.2).

### 2.3.2 Study Sites

Sampling was done in the Gulf of Maine during the summer of 2010 during a coastal cruise and several day trips (Fig 2.1). The day trips were conducted from the Darling Marine Center (DMC). One of the sites (DMC-2) is visited bimonthly in a time series and lies 5 nautical miles from the mouth of the Damariscotta Estuary. Near the mouth of the estuary is DMC-short and 20 nautical miles off the coast is DMC-Far. These sites were visited in early and late summer. All other sites were visited during a coastal survey during late summer. The cruise followed several transects oriented from nearshore to offshore. Since the multiple replicates were time consuming, only a few sites could be chosen; thus effort was divided between deeper waters offshore and shallow ones nearshore.

## 2.4 Results

Table 2.1 summarize collection data for the sample sites visited during the 2010 field season. There were 3 sites sampled in early summer (May & June) and 8 sampled in late summer; each group is ordered by increasing depth. The shallowest site visited was DMC Short at 53 meters and the deepest was WB-7 at 238 meters. The number of replicates taken for each site and date ranged from 6 to 20. Although 144 samples were collected in total, the table depicts the 123 that were processed; 1 sample was lost and it was decided that the 20 others would not provide sufficient additional information.

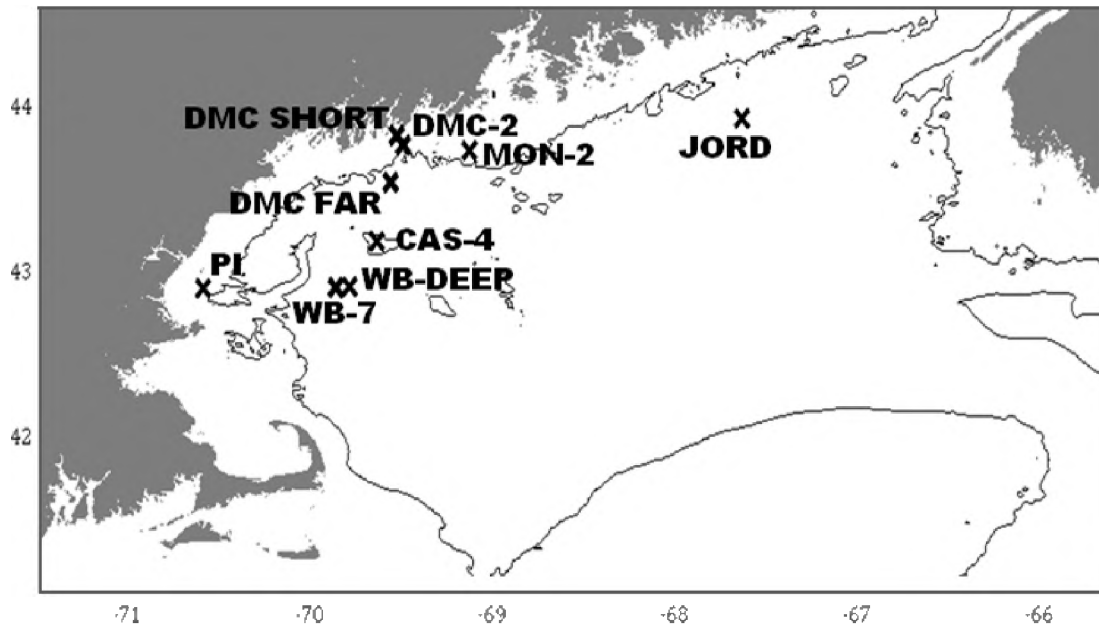


Figure 2.1. Gulf of Maine. Sample sites visited on day trips and through a coastal survey during the summer of 2010, latitude and longitude are indicated on the axes

Temperature profiles indicated that the surface was much warmer than the water column at depth, which results in a higher mean temperature for the top 40 meters than the entire water column. This was found for every site, but WB-7 showed the greatest difference in mean temperature between the top 40 meters and the entire water column (4.1 °C) compared to a difference of 0.6 °C at DMC Short. The pattern of temperature difference follows the site depths with the deepest and the shallowest having more and less variable temperature profiles respectively.

#### 2.4.1 Abundance Biomass

Mean dry weight of the zooplankton was found for each sample site and date (Fig 2.2(a) & Fig 2.2(b)). The greatest biomass was found at Wilkinson Basin (station WB-7) while CAS-4 was found to have the least. Deeper sites tended to have a greater biomass in the water column, with Jordan Basin being the exception. A noticeable

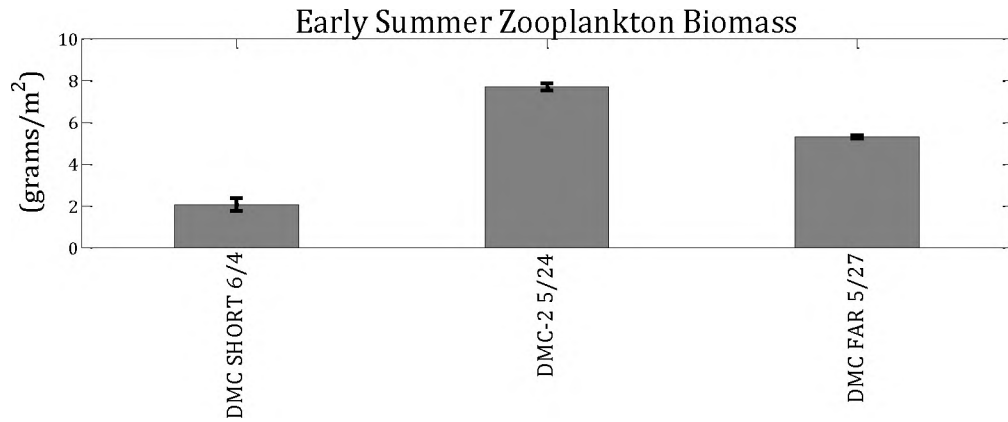
Sample Site	Date 2010	Depth (meters)	Number of Replicates	Top 40 m temp (°C)	Water Column temp (°C)
DMC SHORT	4-Jun	53	12	8.52	7.92
DMC-2	24-May	113	20	7.38	5.74
DMC FAR	27-May	165	16	8.01	5.7
DMC SHORT	27-Jul	53	8	10.33	9.73
MON-2	18-Jul	67	7	11.02	10.13
CAS-4	17-Jul	75	8	10.14	8.2
PI	16-Jul	79	8	9.72	8.17
DMC-2	27-Jul	113	6	11.34	8.96
DMC FAR	30-Jul	165	12	10.86	8.27
JORD	20-Jul	202	8	10.78	8.79
WB Deep	22-Jul	233	10	10.98	7.27
WB-7	16-Jul	238	8	11.28	7.18

Table 2.1. Sample Site Summary. Summary of collections made in 2010 with date, depth, temperature and number of replicates indicated. The ordering of the sample sites is first divided by season (early summer; late summer) and then depth, going from shallow to deep

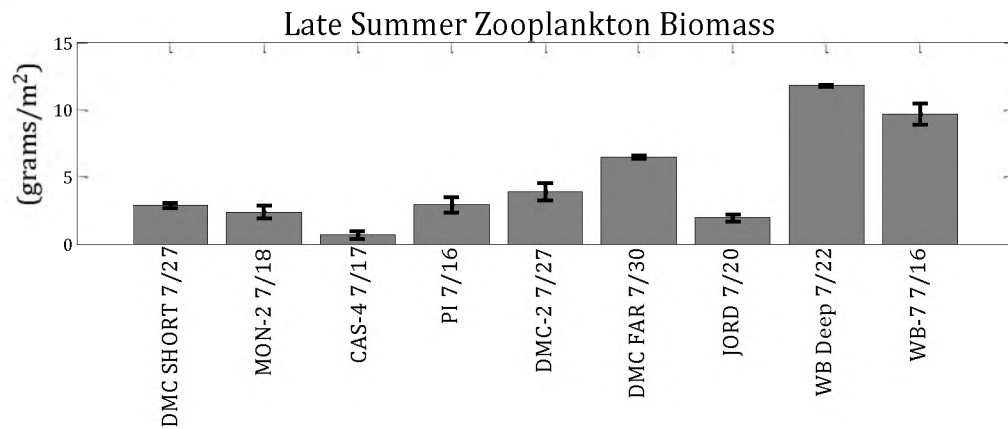
decrease in biomass occurred between early and late in the summer at DMC-2, a less pronounced decline was evident at DMC Far.

#### 2.4.2 Abundance Numbers

*Calanus finmarchicus* from the C1 to adult stage were enumerated, the mean number and standard error have been determined according to sampling site and season (Fig 2.3(a) & Fig 2.3(b)). Since it is the most ecologically important, stage CV abundance is displayed independently (Fig 2.4(a) & Fig 2.4(b)). The overall patterns follow zooplankton biomass: deeper stations tend to have a greater *C. finmarchicus* abundance, especially stage CV. The three sites that were less than 70 meters deep (DMC Short 6/4, DMC Short 7/27, MON-2 7/18) had an especially low number of stage CV in the water column. From early to late summer there was a noticeable decrease in the number of CVs at the deeper DMC stations, despite the high *C. finmarchicus* abundance at DMC-2 in July.

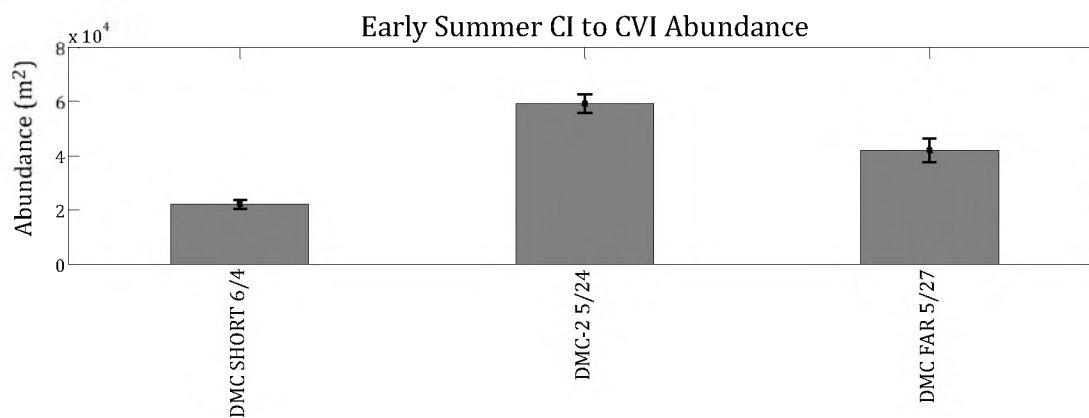


(a) Early Summer Zooplankton Biomass

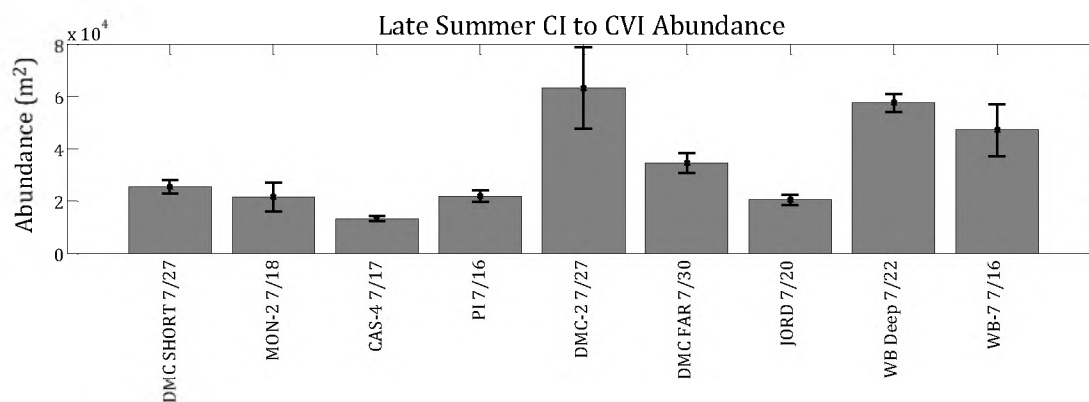


(b) Late Summer Zooplankton Biomass

Figure 2.2. Zooplankton Biomass. Values calculated from the total dry weight of samples collected with vertical tows. a) are the sample sites visited in the Early summer and b) are those from the late summer. All Sample sites and dates are indicated. The bars depict the mean biomass of the water column (*grams/m²*) with  $\pm$  one standard error.

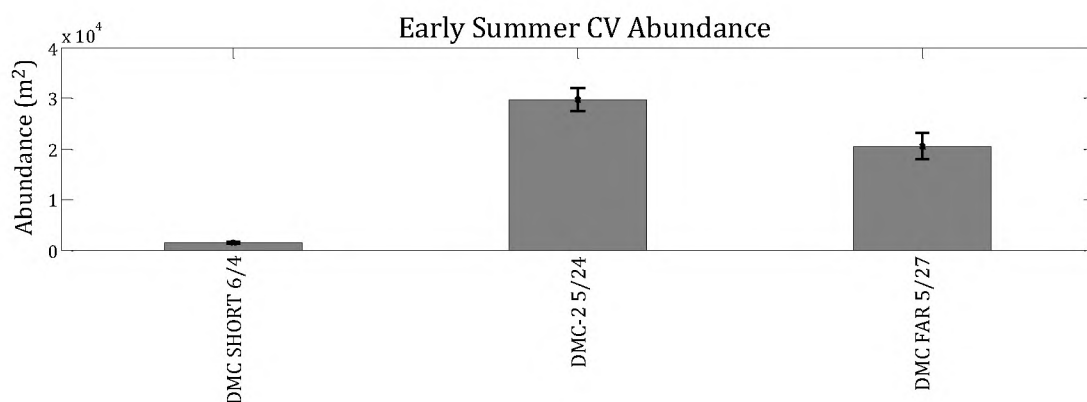


(a) Early Summer *C. finmarchicus* CI to CIV Abundance

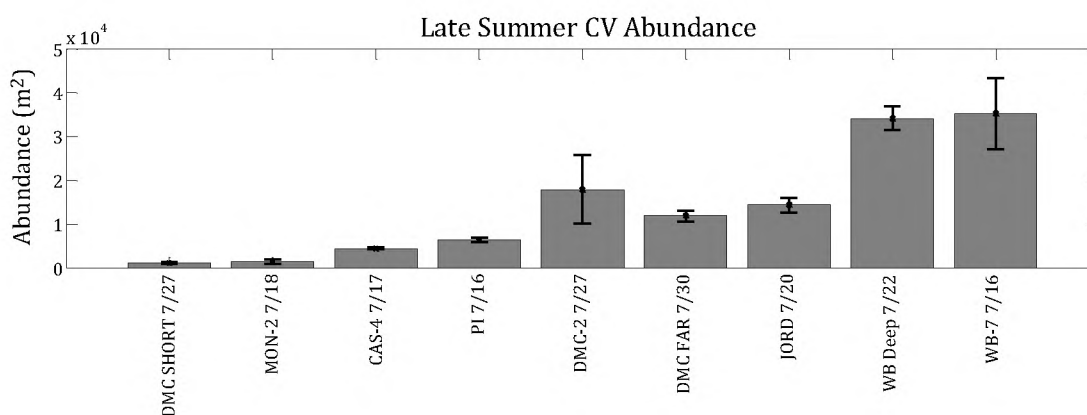


(b) Late Summer *C. finmarchicus* CI to CIV Abundance

Figure 2.3. *Calanus finmarchicus* Abundance of Stages CI to CVI. a) Stations visited in early summer and b) stations in late summer. All sample sites and dates are indicated. The bars depict the mean abundance of the water column ( $number/m^2$ ) with  $\pm$  one standard error.



(a) Early Summer CV Abundance



(b) Late Summer CV Abundance

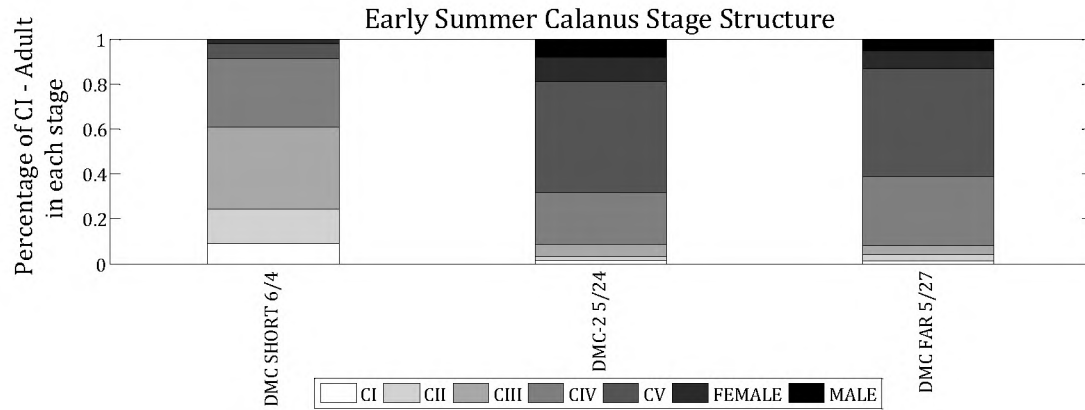
Figure 2.4. Abundance of *Calanus finmarchicus* Stage CV. a) Stations in the early summer. b) stations in late summer. All sample sites and dates are indicated; stations are organized by depth with shallow to deep arranged left to right. The bars depict the mean abundance of the water column ( $number/m^2$ ) with  $\pm$  one standard error.

### 2.4.3 Stage Structure

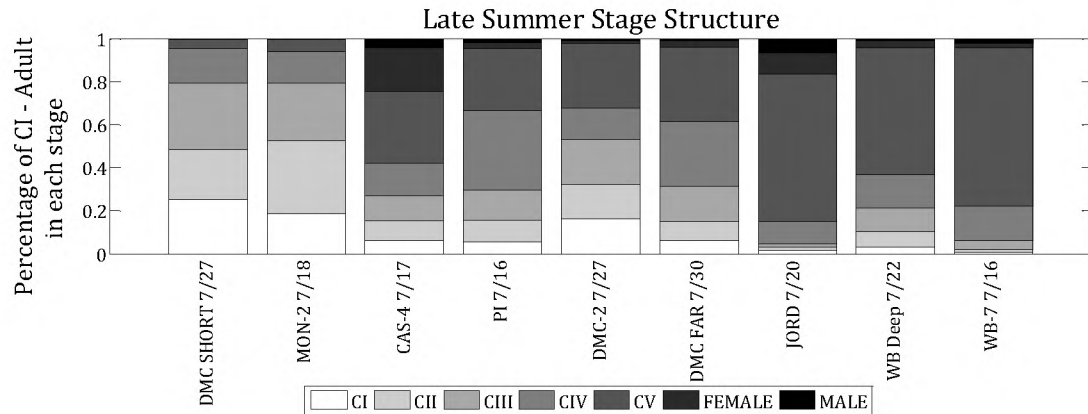
A greater percentage of late stage copepods and adults were found at the deeper stations, while the shallower sites feature younger developmental stages (Fig 2.5). The DMC sites experienced a shift from older to younger stages later in the summer; DMC-2 and DMC Far were the only deep sites (greater than 100 meters) in which the majority population was not comprised of CVs. While adults were still present at DMC-2 and FAR early in the summer, their percentage of the population was marginal during the later sampling dates. The sampling sites located in Wilkinson Basin and Jordan Basin harbor *Calanus finmarchicus* populations in which the CV stage comprises the majority.

### 2.4.4 Mortality

Mortality was calculated for stage pairs at each sample site. Means are displayed in the figures (Fig 2.6). White indicates zero mortality, red positive and blue negative instantaneous mortality with darker shades indicating greater rates. Younger developmental stage pairs are not displayed, but are mostly negative. Much of the late season CV/CVI mortality was greater than 0.2 with the highest being 0.34 at WB-7. The deep late season sites where CVs comprise the majority of the population feature negative CIV/CV mortality between -0.10 and -0.18, these are JORD, WB Deep and WB-7. No temporal or spatial pattern is apparent in the figure, which was confirmed by a statistical test described below.



(a) Early Summer Stage Structure



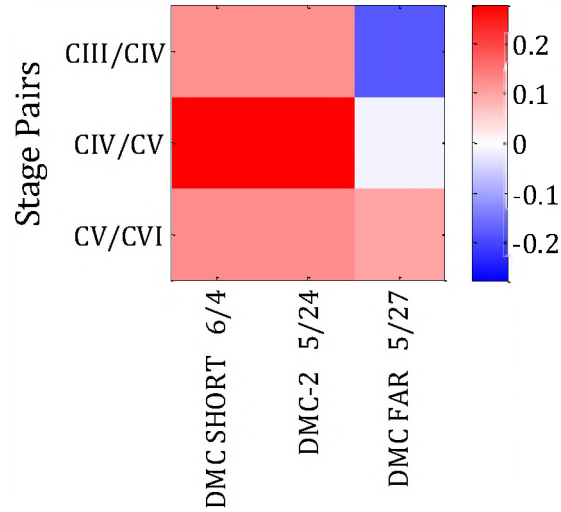
(b) Late Summer Stage Structure

Figure 2.5. *Calanus finmarchicus* Population Structure (Stages CI to CVI). Stage proportions were determined from the mean abundance of each stage at a sample site. a) Stations visited in early summer and b) stations in late summer. All sample sites and dates are indicated. The grey scale shading corresponds to the stage depicted in the legend.

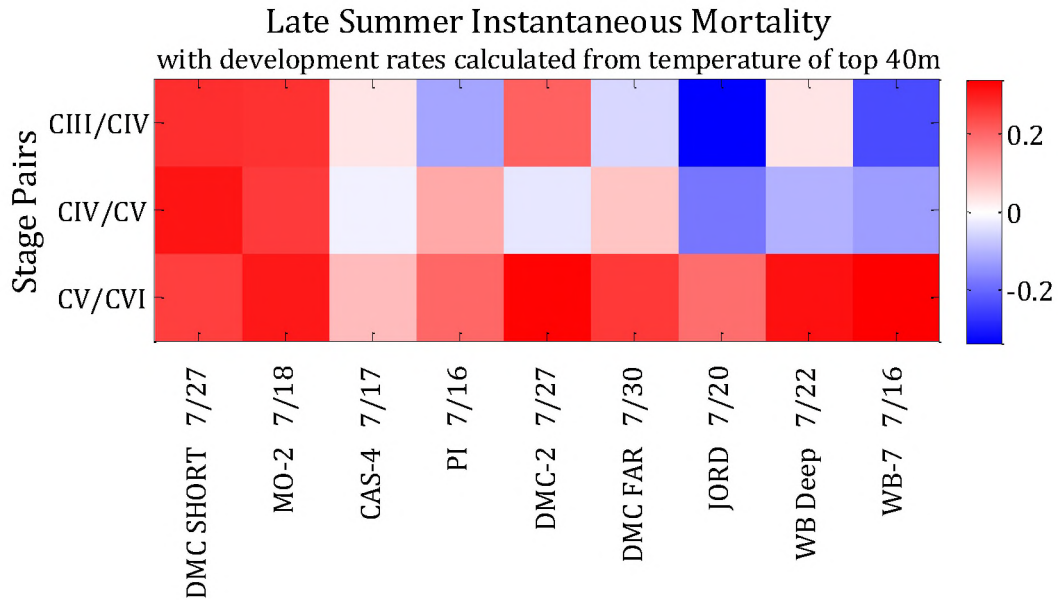


### Early Summer Instantaneous Mortality

with development rates calculated from temperature of top 40m



(a) Early Summer Mortality



(b) Late Summer Mortality

Figure 2.6. Estimation of *Calanus finmarchicus* Mortality with VLT Method. Using the VLT method, instantaneous mortality ( $1/day$ ) was calculated for the joint stages CIII/CIV, CIV/CV, and CV/CVI using stage abundances of the replicates and the mean water temperature of the top 40 meters to calculate development times. Stations visited in early summer a) and stations in late summer b). All sample sites and dates are indicated. The color scale shading corresponds to the mortality rate with red being positive, blue negative and white zero; darker shades indicate higher values as depicted by the legend bar.

A multifactor analysis of variance was performed using two factors in a fixed and crossed unbalanced design (Table 2.2). The first factor was depth with sample sites at less than 100 meters considered ‘shallow’ and those greater ‘deep.’ The second factor was season, which was split between samples taken ‘early’ in the summer (May and June) versus those taken ‘late’ in the season (July and August). There was 1 sample site early and shallow, 2 early and deep, 4 late and shallow, 5 late and deep. The test revealed only one significant difference, a p value of 0.039 for the CV/CVI joint stage indicates the mortality rates early in the summer were statistically different from those found later on.

	CIII/CIV	CIV/CV	CV/CIV
Depth	0.737	0.738	0.669
Season	0.658	0.229	0.039

Table 2.2. Multifactor ANOVA. p-values from the multifactor ANOVA of Depth and Season for each of the joint stage pairs.

#### 2.4.5 Power Analysis

The numerous replicates provided an opportunity to do an analysis for an optimal sample size of net tows, this was done using a bootstrap approach. The variable being investigated is stage ratio rather than abundance. It could have been done with replicates from any sample site, but the one chosen is DMC FAR in May, with the CV stage ratio. The CV stage had the greatest variability across sites. The site was chosen since it had the second most replicates after DMC-2 with 16, but lacked outliers. Thus, the replicates provided a good distribution of possible CV stage proportions. The mean CV proportion was 0.481 with a standard error of 0.014. The mean CV proportion was also found for 10,000 bootstrap samplings with replacement. These bootstraps were performed for each subsample size ranging from 1 to 16. The distance of the bootstrap mean and original mean was calculated and placed in a bin corresponding to its subsample size (Fig 2.7(a)). It was further calculated what the maximum distance would

be, given a subsample size; this distance is the one way 95% confidence interval of the distribution formed from the bootstrap differences. Thus, there is a 5% chance that the difference between the true mean and the mean found from the indicated subsample size will be greater than the corresponding maximum difference (Fig 2.7(b)). Both figures indicate that as the number of subsamples increases the distance from the mean is rapidly reduced, but then flattens out, with each additional subsample yielding progressively fewer gains.

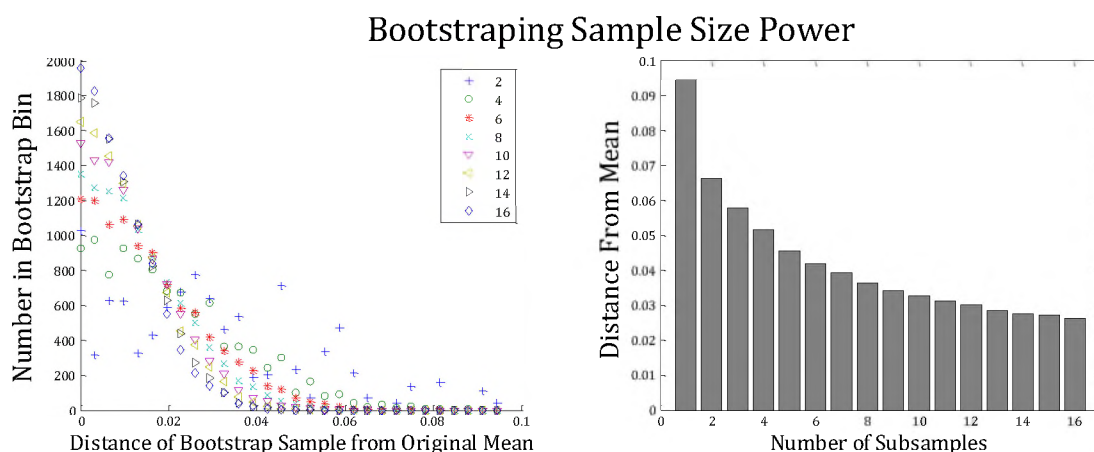


Figure 2.7. Bootstrap Power Analysis. a) The figure on the left depicts the number of bootstrap samples binned into distance from the mean. Distance from the mean refers to difference between the original sample proportion mean, and the mean proportion found from the subsample. The even subsample sizes from 2 to 16 are displayed. b) The figure on the right displays the 95% limit of distance from true mean for the number of replicates used.

## 2.5 Discussion

Zooplankton have been studied in the Gulf of Maine for over a century (Bigelow 1924) and much of that work has focused on *Calanus finmarchicus* as the most ecologically significant species in the community. However, most studies have been concerned with the populations inhabiting Georges' Bank and the deep basins, and few have sought to observe the inner shelf (Runge and Jones 2012). Thus, the results presented here adds valuable knowledge on the demography of *C. finmarchicus*.

The data corroborate previous findings of differences in *C. finmarchicus* stage structure between the inner coastal shelf and deeper offshore waters (Runge et al., 2012) and observations of very high abundances of stage CV (presumably dormant) in Wilkinson Basin (Melle et. al. submitted). Runge et al. (in preparation) observed a significant relationship between depth and abundance for the late stages (CV–CIV), but not for the early stages. These results are consistent with my finding that deeper sampling sites harbor a greater proportion of the population in late development stages. Overall abundance is lower at the nearshore sites especially for the larger late stages, which is readily observed in the stage structure dominated by younger copepodites. A time series analysis provided by Runge et al. (2012) indicates that *Calanus finmarchicus* typically reaches its abundance peak in September followed by a sharp decrease. The observation of 30 to 40 thousand CV copepods per square meter at the WB stations demonstrates that the basin can host an incredible abundance, which may increase through September. The processes we are concerned with in this study are not easily observed, but can be supported by an analysis of patterns. Differences in the community assemblage over time and space can indicate species specific patterns, the same approach can be utilized to discern processes affecting specific stages. Here I assess two hypothesis for explaining the observed abundance patterns and stage structure on the inner shelf and deep Wilkinson Basin. The lipid rich CV stage could be preferentially targeted by numerous visual predators in nearshore waters (Runge et. al 2012) or they might be advected to the deeper basins where they can enter diapause (Maps et al. 2012)

Mortality derived predation is a possible mechanism for explaining the observed abundance and stage structure pattern of *Calanus finmarchicus* in the Gulf of Maine. The population during the summer is dominated by the CV stage which are ready to enter diapause, but the inner shelf sites are too shallow for CVs to migrate to depth. Considering their relatively large size and visibility, these copepods would be easily detected by visual predators. Furthermore, diapausing *C. finmarchicus* are in a state of

reduced metabolic activity and would not exhibit escape behaviors, making them easy prey. According to life history theory the diapausing behavior provides an adaptive advantage for *C. finmarchicus* since they are able to avoid particularly hazardous times of the year when migrating to depth. The shallow water of the inner shelf has the consequence of making *C. finmarchicus* more susceptible to abundant predators such as larval fish and planktivorous. Generally, smaller zooplankton are distributed in the nearshore waters, an observation Frank (1987) used to support his finding of fish larva concentrating where food is abundant. Predation also tends to be greater in shallow waters inhabited by invertebrate predators such as cheatognaths, but they don't preferentially target larger copepods. However, there are a greater number of visual predators in the summer months, together these sources of mortality can account for the lower overall abundance and stage structure skewed towards younger copepodites.

An alternative hypothesis proposes that the WMCC advects late stage *Calanus finmarchicus* offshore into deeper waters and basins where they can enter diapause. Considering that the current flows faster towards the surface it is unclear how this mechanism would target the later stages occupying deeper water. Comparing the early to late summer sampling sites at the DMC reveals a decrease in CV abundance at the deep sites, but no such decrease occurs at the shallow site. The 53 meter deep, DMC Short site featured very few late stages during both sampling times. Perhaps advection is responsible for removing some of the CVs at the deeper DMC sites, but it is apparent that late stage *C. finmarchicus* cannot survive at all at the particularly shallow sites. The coastal current could also help explain the higher abundances offshore, however with either of these advection scenarios the connection is likely to be indirect since currents typically follow isobaths (Pringle 2006).

The predation and advection hypothesis for the observed *C. finmarchicus* demography have been suggested elsewhere (Runge and Jones 2012; Runge et al., 2012; Maps

et al., 2012), but it was the goal of this research to further evaluate them through estimation of mortality. Apart from indicating higher CV/CVI mortality in the late summer compared to the early summer, the VLT method and multifactor ANOVA failed to identify any cross shore or depth pattern. The 100 meter grouping division was chosen because it corresponds to that isobath, but several other variation were tried and yielded no better results. Furthermore, the one significant relationship was found with data which may have resulted from a violation of assumptions and does not actually exist. The VLT method uses development times along with stage abundances to calculate mortality, but these times are based on observed temperature profiles and laboratory derived development functions. The function does not account for diapause and in the late summer most of the CVs are in a state of arrested development. The buildup of CV stage abundance is interpreted by the VLT method as high CV/CVI mortality and low CIV/CV mortality. The negative mortality rates in the joint CIII/CIV stage indicates that other assumptions were also being violated. Although the VLT method is supposed to be a robust means of measuring mortality its assumptions are commonly violated and it cannot be utilized in many situations (Gentleman et al., 2012). This study was careful to adhere to the requirement of repeated replicates to reduce the influence of sampling variability. Plourde and others (2009) decided that rather than using replicates they would find the mean of multiple transects for an entire regions. They sacrificed some spatial resolution but were able to show that different regions exhibited their own mortality patterns according to stage.

The focus on multiple replicates at a few sample sites has had the counterintuitive effect of reducing statistical power when it came to finding spatial and temporal patterns. In the multifactor ANOVA there were only 12 sample means divided amongst 4 groups, two for the early and late summer and another two based on depth. Consequently, a small number of samples were in each group, making it unlikely to find any relationship with the analysis of variance. Aksnes and Ohman (1996) emphasize replicates when

using the VLT method because of the concern over sampling variability, which could skew mortality estimates. As discussed in the introduction, patchiness has long been a concern for oceanographers and there is a wealth of evidence for sampling variability. However, there is some support for a higher degree of variance in biomass than in the community structure (Winsor and Clarke 1940). The power analysis done in this study indicates that the benefit of multiple replicates quickly diminishes when considering stage proportions. Therefore, rather than doing extensive replicates, sampling effort should be distributed spatially and temporally. Here, it seems that 4 replicate samples with the dual ring net would have been sufficient for each station, and would have enabled effort to be diverted to more sites. Regardless of the VLT and mortality estimates, the demographic information provides insights into the population dynamics of *Calanus finmarchicus*. The data presented here suggests that predation along with bathymetry and water circulation are important influences on copepod population dynamics.

## **Chapter 3**

### **MORTALITY ESTIMATION UTILIZING THE STRUCTURED POPULATION MOLTING RATE METHOD**

#### **3.1 Introduction**

Copepod populations form vital links in the marine ecosystem, connecting phytoplankton production to species of concern in higher trophic levels. Knowledge of the population dynamics of copepods enables formulation of models for forecasting species distribution and abundance. However, depending on the species, location, and time of year, copepod population growth rates can vary significantly, and improvements to population models require the accurate description of diverse life-histories (Ohman et al., 2004). Although understanding all aspects of a species' demography is important, mortality remains the primary limitation in population models (Runge et al. 2005). Mortality cannot be measured directly, and is a challenge to estimate with current methods that require limiting assumptions (Aksnes et al., 1997). Here we develop a new method for calculating mortality, the Structured Population Molting method (SPM). As an extension of the Vertical Life Table approach (VLT) introduced by Ohman and Aksnes (1996), the SPM confronts many of the assumptions and limitations of the VLT through the direct observation of molting rates in batch incubations.

##### **3.1.1 Vertical Life Table Method**

Utilizing stage distribution data and established development rates, the Vertical Life Table (VLT) method estimates mortality of successive stage pairs. It assumes that all individuals in the sampled population have experienced the same environment, and have equivalent histories. Thus, the VLT method ignores the issue of advection by assuming upstream populations are identical to local populations (Aksnes and Ohman 1996). The mortality calculation of the VLT requires information on the development



rates for two adjacent stages and the ratio of relative abundance between them, but not the absolute abundance. Development time for each stage at ambient water temperature is typically estimated from empirical relationships derived from laboratory experiments. Campbell et al. (2001) established such a relationship with *Calanus finmarchicus* using the Belehradek temperature function, which has been done for other copepod species as well.

Recognizing the ease of use of the VLT method and its relaxation over advection concerns, many oceanographers have adopted it for a variety of copepod species in several regions (e.g. Ohman et al., 2002; Hirst et al., 2007; Ohman et al., 2008; Hirst and Ward 2008). While we are interested in *C. finmarchicus* for method development here, the technique is applicable to any population with a well defined stage structure. Aksnes and Ohman's (1996) trial of the method was based upon *Pseudocalanus newmani* in coastal waters off Washington state (USA), a species that would see further attention along with *Calanus finmarchicus* on Georges Bank in the coastal northwest Atlantic Ocean (Ohman et al., 2002). Likewise, *Calanus helgolandicus* mortality was estimated within the English Channel (Hirst et al., 2007) and *Calanus pacificus* rates were measured in the California Current System (Ohman et al., 2008). Hirst and Ward (2008) further expanded the reach of the VLT method by applying it to the ubiquitous cyclopoid copepod, *Oithona similis*, in the Scotia Sea and Southern Ocean. These studies and others have enabled the comparison of mortality rates among species, regions and different life stages with the capacity for even smaller scale analysis. For example, Plourde et.al. (2009) investigated regional differences in mortality of *Calanus finmarchicus* in Canadian waters of the northwest Atlantic. Generating this higher resolution of mortality is vital for accurately determining the abundances of zooplankton populations in a variety of environments (Verity and Smetacek 1996).

The expanding application of the Vertical Life Table owes much to the recognized importance of mortality in population dynamics and the desire for an uncomplicated, robust method. However, prior to its wholesale adoption, a careful consideration must be given to the assumptions upon which the VLT is founded. Gentleman et al. (2012) provide a thorough analysis of these assumptions, identifying possible sources of error in the application of the VLT. Although the VLT does not require that a population be tracked over time despite advection, it is assumed that the successive stages sampled have experienced an equivalent environment and transport for at least the duration of those two stages. There also should not be any trend in recruitment to any stage over that time; otherwise Gaussian noise in recruitment will not even out with repetitive sampling (Aksnes and Ohman 1996).

Concern over sampling noise within the stage ratios led Aksnes and Ohman (1996) to advocate for a minimum of 6-10 replicates when using the VLT. Countering this random variation in recruitment and stage ratios workers have combined samples within a transect and treated them as replicates (e.g. Plourde et al., 2009). It is advised that this tactic only be done when samples are taken within a time interval less than the duration of two developmental stages (Aksnes and Ohman 1996; Ohman et al., 2002). Eliminating all other factors, the observed differences between stages must be due to mortality and development times.

When considering the development times used in the calculation there are reasons to question the application of Belehradek temperature functions to pelagic populations (Gentleman et al., 2012). Campbell et al. (2001) had reared *Calanus finmarchicus* from eggs in controlled experiments at three temperature settings, and excess food availability. Tracking the progression of the culture through stages and relating the data to the temperature regime through the Belehradek temperature function provides a means of estimating development time for each stage at a given temperature. These estimates of development time assume that the copepods are not food limited,

that the rate of development is reflected by the water temperature sampled; and that they are proceeding through the development stages as they had in the laboratory setting.

The temperature question is one that remains unresolved and unstudied in marine copepods. It is well recognized that copepods of different stages are characterized by different vertical distributions. Furthermore, copepods perform diel vertical migrations (DVM) in order to avoid predators and access better food. However, not all stages behave in the same manner; many of the younger calanoid stages remaining at the surface while the late stages migrate (Fisken and Carlottii 1998; Hays 2003). Due to possible strong gradients in temperatures between surface and deep waters, there is no obvious temperature regime experienced by all copepods. The contemporaneous ambient temperature may not be as influential as the cumulative temperature history experienced by an individual (Gentleman et al., 2012). Entomologists have long recognized this effect, establishing degree days as an integrative measure of temperature history for commercially important species. Many workers who have applied the temperature development function on calanoid populations have to rely upon their own judgment as to what temperature to use, which is often an average of the upper water column (e.g. Plourde et al., 2009).

The issue of food limitation has already received much attention in regards to its affect on both development times and growth rates. Campbell et al. (2001) found that copepods treated with lower food quantity exhibited decreased size and condition in comparison to the higher food levels. Importantly, development rates through stages were likewise affected, although not to the same extent as growth rates. Stage durations at low food were on average 1.5 to 2 times longer than durations at high concentrations, an observation that has been utilized in ad hoc corrections of the functions application (e.g. Hirst et al., 2007). Also of concern is the greater variability of stage distributions with decreased food availability; we can expect that any estimations made under food limitation will contain large confidence intervals. These experiments as well as

others indicate that sustained limited food availability will significantly slow development (Campbell et al., 2001; Wagner et al., 1998). However, studies have suggested that over a short time period after capture or removal from culture into a food limited environment, copepods will develop normally into the subsequent stage (Miller et al., 1984; Shreeve et al., 1997). Miller et al. (1984,1993) has suggested that this observation is due to individuals receiving hormonal signals relatively early in the stage and effectively reaching a threshold after which molting is inevitable.

The deviations towards faster or slower development still describe a population in a constant growth period, an assumption violated by many copepod species through a variety of dormancy behaviors (Dahms 1995). In many *Calanus spp.* diapause is characterized by an ontogenetic vertical migration to depth, reduced metabolism and arrested development in the CV stage (Hirche 1996). The departure of *Calanus* from direct development violates the Belehradek temperature function and can potentially bias any mortality results stemming from it. Thus, in any estimation of mortality a further examination and accounting of diapause is warranted.

### **3.1.2 Deriving Development**

The importance of accurate development times for estimation of mortality provides motivation for development of alternative methods such as direct assessment. For copepod life histories, there are essentially three ways of determining development rates: laboratory cultures, direct observation of molting rates and tracking a natural cohort over time. Similar to horizontal mortality methods, the latter technique does not directly measure development, but rather derives it by fitting observations to the model (Shreeve et al., 1997). In contrast to the laboratory method (Campbell et al., 2001), the direct observation method represents an *in situ* estimation technique using short experimental durations and fewer restrictions (Shreeve et al., 1997).

Sorting of individual copepods as a direct means of observing molting rates was first described by Burkhill and Kendall (1982). In this approach, a sample of copepods is sorted from a free-living population and then tracked individually over short durations to observe the fraction molting (Shreeve et al., 1997; Aksnes 1997). Miller et al. (1984) had raised concerns regarding handling effects when he utilized the method. He detected what was described as a molting burst (elevated molting activity), attributed to the shock of handling. Although acknowledging the possibility, the molting burst effect has been deemphasized in later studies (Shreeve et al., 1997; Peterson et al., 1991). Assuming consistent molting behavior pre- and post capture, Runge et al. (1985) measured molting rates of *C. finmarchicus* that were consistent with change in the population's stage structure over an 8 day period. Although direct observation of individuals is an effective means of observing molting it is labor intensive; it requires observation of a large number of individuals to obtain reasonable confidence intervals for estimates of development time (Miller et al., 1984).

A variation of the direct observation method that provides the foundation for our own procedures is the batch incubation, first attempted by Tranter (1976) and used later by Kimmerer and McKinnon (1987). The straightforward method represents an *in-situ* incubation and requires little specialized equipment and minimal additional labor. Tranter (1976) size fractionated a live zooplankton sample so that unwanted larger and smaller species or stages were excluded, a technique known as the artificial cohort method. A subsample of the cohort is taken at the onset of the incubation and then at some later period of time (Kimmerer and McKinnon 1987; Peterson et al., 1991). While investigating incubation duration, Kimmerer et al., (2007) suggested a time interval that was no more than the duration of the target life stage. If the duration was longer, an individual copepod may advance two stages without recognition. Furthermore, shorter incubation times would minimize bottle effects that may accumulate as the experimental conditions

deviate more from natural conditions over time (Kimmerer et al., 2007; Hirst et al., 2005), such as reduced oxygen, excess  $CO_2$  and increasing risk of bacterial blooms or disease outbreaks.

Shreeve et al. (1997) conducted a review of the principal methods attempting to resolve remaining issues. They found that despite differences in methodology, no significant differences could be found among the resulting development times. Development time ( $D$ ) of the stage was ( $i$ ) calculated from the inverse of the molting rate ( $MR$ ), such that  $D_i = 1/MR_i$ . However, deriving development times from these methods is inappropriate because the calculation wrongly assumes that the age distribution within each stage is uniform. Hirst (2005) identified this error, noting that the age distribution of a stage with constant recruitment is closer to a gamma distribution and will be skewed toward younger individuals. The skew is due to instantaneous mortality and the lower survivorship of older individuals. Thus, development times calculated from the inverse of molting rates would be overestimated. Although, it is ill advised to use molting rates in place of development times, the direct observation methods described here remain useful for parameterizing the population. While the VLT method estimates mortality using development times, this paper develops the Structured Population Molting method that uses molting rates measured in the field.

### **3.2 Methods**

For a description of the study location and sampling protocols refer to Chapter 2 of this thesis (2.3).

### 3.2.1 Direct Observation of Molting in Incubations

#### *Incubation experiment*

Batch incubations for the direct observation of molting were performed at 7 of the 12 sampling stations (Table 3.1). The methods here are similar to those of the artificial cohort described earlier, but without size fractionation of the sample through sieving. The target species, *Calanus finmarchicus*, dominates the zooplankton community at the sample sites and the additional handling step was unnecessary. The following is a description of the basic experimental procedures. Modifications were made to improve the method as the field season progressed, and recommendations for an ideal set up are suggested here.

	DMC-2	DMC-FAR	DMC-SHORT	PI	WB-7	CAS-4	MON-2	JORD	WB-D
May	<b>20</b>	<b>16</b>	<b>20*</b>	0	0	0	0	0	0
July	<b>12</b>	<b>14</b>	12	8	8	8	<b>8*</b>	8	<b>16</b>

Table 3.1. Incubation Sample Sites. Number of replicates depicted with bold numbers indicate locations and times where an incubation was done, but (\*) asterisks mark where molting rates were unattainable.

#### *Transfer to incubation containers:*

Zooplankton samples were collected with a net tow at seven sites that were also to be used in the Mortality study (Table 1). Depending on the abundance of zooplankton a full parabolic tow was made or the net was dropped and then raised while under way (<1 Kt) to collect half of the parabolic tow. The animals were collected in a ‘live’ cod end modified to retain seawater and plankton. Upon completion of the tow, the live zooplankton sample was distributed among incubation chambers. This step underwent several modifications, ideally a subsample would be taken of the diluted live sample with a stempel pipet, but I used a swirl and pour technique and later a large bore pipette. It is important that overcrowding not occur, since it would increase the risk of bottle effects. The number of *Calanus finmarchicus* incubated in each container during the

initial experiment (DMC 2; May 24, 2010) ranged from 470 to 1040, in later incubations the number remained at the lower bound of that range. The incubation containers were 3.8 L polyethylene terephthalate plastic food storage jars with water tight lids. Gelatinous macrozooplankton, larval fish, euphausiids and amphipods were removed from the container if found, but this was rarely an issue. The containers were usually filled with surface water, but subsurface water is preferable. They were kept in a cooler on the boat, and upon return from the trip they were transported to a temperature controlled cold room. As the season progressed and the surface water temperature rose it was decided that during transport the cooler should be chilled with ice.

#### *Control and Treatment:*

Half of the 14 live zooplankton containers were selected as the incubation treatment and half were selected as the control. The difference in stage structure between the sets is the observed molting rate from the *start* of the incubation until it *finished*. The control samples would be fixed at a 4% formalin concentration in a manner identical to the previously described sampling protocols. For the first three incubations conducted in May, fixing the control was not done until 2 to 3 hours after the live tow when the boat returned to dock and the live containers were moved to the lab. Later the samples were fixed immediately after the live tow, while on board the research vessel. The time of fixing signified the start of the 48 hour incubation period after which those containers would be transferred to archival glass jars and treated with formaldehyde.

#### *Analysis:*

Counting and staging of the incubation treatments followed similar procedures set out earlier for the zooplankton taxonomic analysis (Chapter 2 methods [2.3](#)). However, I was solely interested in the stage structure and not the abundance, thus no effort was made to use methods that would provide abundance estimates. When samples were too dilute for measured aliquots to be of use, subsamples were taken with glass pipets rather than stempel pipets. Although, the count requirements were set the same



as the demographic analysis, with 200 being the minimum total, some of the containers held less *Calanus finmarchicus* than this, with the least being 156. Two of the seven incubations were discarded because the presence of *Calanus* in the live sample was limited, these sites (MON 2 and DMC short) were near shore and shallow.

### 3.2.2 Calculations

Variations of the direct observation method use the same fundamental calculation to measure molting rate (e.g. Peterson et al., 1991).

$$MR_i = \frac{\sum_i^{i+1} N_{i+1,f} - \sum_i^{i+1} N_{i+1,s}}{N_{i,s}} \quad (3.1)$$

Equation (3.1) sums the ratios from the stage of interest ( $i$ ) to the final adult stage (11): Molting Rate ( $MR$ ) of the stage ( $i$ ) is a function of the abundance ( $N$ ) at the start ( $s$ ) and finish ( $f$ ) of the incubation. The equation (3.1) reduces to the one below (3.2) when considering the final molting rate of adults ( $MR_{10}$ ).

$$MR_{10} = \frac{N_{11,f} - N_{11,s}}{N_{10,s}} \quad (3.2)$$

I made a variation on equation (3.1) by starting with the final stage and working backwards, without the summation. The ending abundance of a stage is a function of the previous stage structure, molting rates, and incubation time. The molting rate of stage CV into adults can be found from equation (3.2). The molting rates into juvenile stages can subsequently be calculated with equation (3.3).

$$MR_i = \frac{N_{i+1,f} - N_{i+1,s} + N_{i+1,s} * MR_{i+1}}{N_{i,s}} \quad (3.3)$$

As recognized by Gentleman et al. (2012), the direct estimation of molting rates presents a unique opportunity when using the vertical approach to calculating mortality. They point out that the VLT formula's structure was restricted by the need to estimate

recruitment through the stage durations established in laboratory experiments under constant environmental conditions. Aksnes et al. (1997) remind us that the VLT and other formulas that are used to solve for stage-structured population parameters, come from the understanding that instantaneous changes in stage abundance are based on the combined effects of recruitment, maturation and death (Eq 3.4).

$$dN_i/dt = R_i - R_{i+1} - m_i * N_i \quad (3.4)$$

In equation (3.4),  $(dN_i/dt)$  is the change in stage  $i$ , with time;  $R_i$  is recruitment into stage  $i$ ;  $R_{i+1}$  is recruitment into the next stage, both represent a change in the number of individuals per day ( $day^{-1}$ ); while  $m_i$  is the instantaneous mortality rate for that stage ( $day^{-1}$ ). Recruitment to the next stage ( $i + 1$ ) is equal to the number in the current stage  $N_i$  that will be developing on into the next at the rate  $MR_i$ , so that  $R_{(i+1)} = MR_i * N_i$ . Likewise recruitment of adjacent stages is related by the equation:  $R_{(i+1)} = R_i e^{-m_i DT_i}$ . These equations have been used for further calculations, but are no longer a necessity when molting rates are measured through direct observation. In vertical approaches, it is assumed that the stage structure represents a stable population and that the parameters are consistent, which enables setting  $dN/dt = 0$ . A full description of the VLT function can be found in Aksnes et. al (1997) and Gentleman et al. (2012). Its derivation, depicted in the equations below(3.5, 3.6), allows the calculation for mortality of joint copepidid stages.

$$\frac{e^{m_i DT_{i-1}}}{1 - e^{-m_i DT_{i+1}}} = \frac{N_i}{N_{i+1}} \quad (3.5)$$

$$m_{C5-C6} = \frac{\ln[N_{C5}/N_{C6} + 1]}{DT_{C5}} \quad (3.6)$$

Equations 3.5 & 3.6 come from the Vertical Life Table method for estimation of instantaneous mortality for joint stages (Aksnes and Ohman 1996). The first equation is for juvenile stages (C1-C5) and the 2nd is for the pre-adult and adult stage (C5/C6), where  $R_{C6+1} = 0$ .  $m$  ( $1/day$ ) is instantaneous mortality,  $D$  is the development time in days, and  $N$  is the stage abundance, which becomes unitless.

Through the incubation experiments we are measuring molting rate ( $MR_i$ ), which is a rate ( $day^{-1}$ ) and thus related to recruitment into the next stage ( $R_{i+1}$ ). Through this, the basis for the VLT calculation and the need to link subsequent stages becomes unnecessary. Referring back to our original equation (3.4) describing population change and following the assumption for vertical methods of a stable population structure, we set  $dN/dt = 0$  and solve for mortality. The derived SPM equations (3.5, 3.6) can solve for mortality using the observed molting rates and stage structure.

$$dN_i/dt = R_i - R_{i+1} - m_i * N_i$$

$$\text{With: } R_i = MR_{i-1} * N_{i-1} ; R_{i+1} = MR_i * N_i$$

Set  $dN/dt = 0$ , assuming stable population structure

$$m_i * N_i = MR_{i-1} * N_{i-1} - MR_i * N_i$$

Simplifying the equation we get:

$$m_i = MR_{i-1} * N_{i-1}/N_i - MR_i$$

### 3.3 Results

#### 3.3.1 Development Times

Stage	Calculation	DMC-2 24-May	DMC FAR 27-May	DMC-2 27-Jul	DMC FAR 30-Jul	WB DEEP 22-Jul
<b>CII</b>	<i>Water Column</i>	4.5	4.5	3	3.3	3.7
	<i>Top 20m.</i>	3.3	2.6	2	2	1.7
	<i>Incubation</i>	NaN	0.355	0.277	0.268	0.337
<b>CIII</b>	<i>Water Column</i>	5.7	5.7	3.8	4.1	4.6
	<i>Top 20m.</i>	4.1	3.3	2.5	2.5	2.1
	<i>Incubation</i>	0.198	0.229	0.164	0.165	0.325
<b>CIV</b>	<i>Water Column</i>	8.6	8.6	5.7	6.2	7
	<i>Top 20m.</i>	6.2	5	3.7	3.8	3.2
	<i>Incubation</i>	0.111	0.035	0	0.089	0.239
<b>CV</b>	<i>Water Column</i>	16.2	16.2	10.8	11.7	13.2
	<i>Top 20m.</i>	11.7	9.4	7	7.2	6
	<i>Incubation</i>	0.083	0.043	-0.006	-0.004	0.003
<b>Mean Temperature</b>						
	<i>Water Column</i>	5.74	5.74	8.94	8.27	7.27
	<i>Top 20m.</i>	8.25	10.28	13.19	12.87	14.89

Table 3.2. Calculated Development Times. 2010 Sample Sites, with temperature dependent development times (*days*) calculated from Campbell's (2001) equation at mean temperature of the water column and the top 20 meters. Also listed are the calculated molting rates from the incubation ( $day^{-1}$ ), and the mean water temperatures ( $^{\circ}C$ ) at each site.

Development times were calculated using the CTD temperature profiles and the Belehradek temperature dependent development time function (Campbell et al., 2001) at the five sites where incubation experiments were conducted (Table 3.2). The development times are calculated with two different temperature variables established from the mean temperature of the entire water column and the top 20 meters of the water column (Table 3.2). Since the top 20 meters were warmer than the entire water column, the calculate times are far shorter. Molting rates calculated from equation (3.3) are also included in the table with development times (3.2), but cannot be readily converted

without assuming uniform age within stage. However, the molting rates, like the development times, vary depending on the time and location of the sampling. Since naupli were not enumerated and the equation requires abundances from two consecutive stages, the earliest stage for which molting rates could be calculated was CII. The CII's molting rate at **DMC 2; May 24** could not be found through the incubation experiment, because they comprised less than 1% of the total count.

The near zero molting rates observed for stage CV in July indicate that this segment of the population was not developing. Interestingly stage CIV at **DMC2; July 27** also suggest arrested development. Comparing CV Campbell development times to the incubation molting rates for CV we see opposing trends when sample sites transition from early to late summer. As expected with the increasing water temperature the development times decreased, indicating the copepods moved through each stage faster. Contrary to the temperature function the observed molting rates decreased to the point that few *Calanus* would be advancing to the next stage.

The direct observation of molting revealed several unrealistic parameters, including negative or near zero development rates of stage CV in July. When interpreting the resulting calculations, the equations used (3.2,3.3) should be kept in mind. The molting rates are calculated by comparing the ratio of stage counts to total counts before and after the incubation, in these cases the ratios went nearly unchanged. However, small differences in stage ratios produces the unrealistic rates observed. Accepting these values for the mortality calculation becomes problematic for the SPM method (Eq. 3.2.2). If the values are interpret as zero development; a molting rate of 0 going into the adult stage, then multiplying the ratio by 0 results with 0 mortality. To avoid this erroneous conclusion, to avoid similar distortions, and to be consistent, I interpret these extremes as arrested development. I choose a 0.005/*day* molting rate, which was consistent with many of the CV rates, but above zero and reflective of a diapause rate.

### 3.3.2 Mortality

Mortality estimates were calculated with the SPM (Eq. 3.2.2) and VLT (Eq. 3.5) methods using, respectively, the molting rates derived from the incubation experiment and the Campbell et al. (2001) temperature dependent function. Here, the development times are calculated using the mean temperature of the water column. Figure (Fig 3.1) compares instantaneous mortality of each stage and joint stage across the five sample sites. The earliest stage presented is CIII because the SPM calculations cannot be made without molting rates, and in several of the incubations there was a lack of early copepodite stages. Since the VLT only calculates mortality for joint stages, all of those estimates are for VLT while the single stage estimates are for SPM (Fig. 3.1).

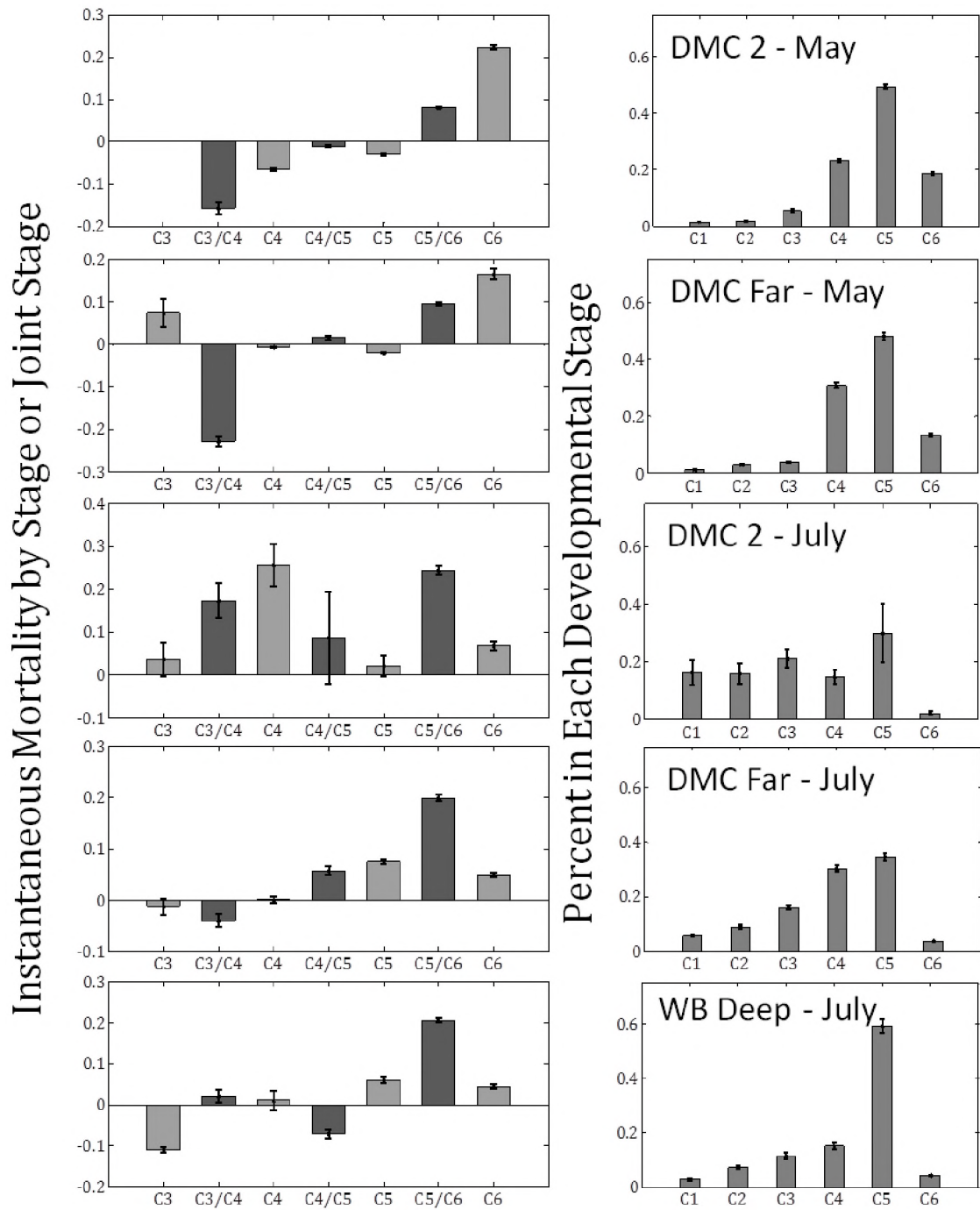


Figure 3.1. VLT, SPM Mortality Comparison. Comparison of mean instantaneous mortality rates ( $day^{-1}$ ) with  $\pm$  one standard error. Dark grey bars are estimations for joint stages based on the VLT method, and using Campbell et al. (2001) temperature dependent development function with the mean temperature of the water column; Light grey bars are the estimations of single stages based on the SPM method and molting rates derived from three incubations. Stage structure is also indicated for each stage at the sample sites and dates which correspond to the adjacent mortality bar graph.

## **3.4 Discussion**

### **3.4.1 Violation of Assumptions**

Negative mortality rates indicate a violation of assumptions which fail to account for some aspect of copepod population dynamics in the calculation. This paper has identified as a source of error the use of temperature development rates for mortality estimates when copepods are not advancing through stages as they would in laboratory settings. The negative mortality rates and stage distribution skewed to later stages suggest that the population at those sample sites is not undergoing constant recruitment, a violation of the vertical approaches' assumptions. The assumption of constant recruitment over long time periods is at some point violated in temperate copepod populations that have seasonal production cycles. Females producing eggs will not do so indefinitely or at constant rates, often resulting in distinct cohort structure. This pulse in the population develops through each of the subsequent stages with a characteristic peak in abundance; to the left of this peak mortality will be underestimated, even negative, while to the right of it mortality will be overestimated. Aksnes and others (1997) have suggested a correction factor in the VLT calculation to account for recruitment trends, but it would require time series data. Proper use of the vertical method demands that mortality estimates be disregarded when such a violation is recognized. However, the purpose of this methods paper is to highlight the differences between the VLT and SPM, and keeping them provides further examples of where they diverge.

Through a sensitivity analysis Aksnes and Ohman (1996) determined that variation in development times was less important to the VLT calculation than sampling variability in the stage structure. Although, their analysis showed the VLT to be robust to gaussian noise, they did not consider disruptions to the general development pattern due to diapause or starvation. The results here suggest that inaccurate development



rates based on the temperature function can bias the mortality estimates. The Belheradek temperature functions are vital, but require ground truthing since laboratory rates are applied to populations in their natural setting. When designing a methodology to detect arrested development in copepods, the need for a robust techniques and the limitations of time and effort must be balanced. The incubation technique provides a cost effective in situ means of eliminating a possible violation of assumptions, particularly for the late stage *Calanus*. The direct observation of molting through the incubation technique accounts for extrinsic environmental variables and intrinsic life history characteristics. The batch incubations provide accurate molting rates and, allow for a new means of calculating mortality. The SPM has the advantage of giving single stage estimates of mortality rather than the constrained joint estimates calculated with the VLT. This not only provides better parameterization of models, but also elucidates ecological differences between stages; combining the CIV/CV stage and the CV/CIV masks the adaptive advantage of the diapause behavior in CV. Furthermore, with clearer distinctions between stages and easily attainable population parameters, comparisons can be made between populations on various temporal and spatial scales. Although, my results cannot be used for such analysis, future studies would have an advantage using these methods.

### **3.4.2 Comments and Recommendations**

Proper control of the ambient water temperature during the batch incubations was a vexing problem for a number of reasons. The temperature of the water column was highly variable from the surface to depths, and the *C. finmarchicus* population is non-randomly distributed through it. Cooler temperatures were sought in this study, but a comparison of warm surface water and cold deep water treatments could indicate a significant effect on the incubation results. However, matching the ambient incubation temperature to that of seawater at a particular depth was not logistically possible.

Furthermore, surface pollution was also a concern and ideally sea water should be pumped from depth, or collected from Niskin bottles.

The work presented relied upon large numbers rather than a controlled experimental settings in order to ensure accuracy. Unlike previous studies which have combined samples over a period of time or within a region to generate replicates (e.g Ohman et al., 2004; Plourde et al., 2009), I focused on individual sites. Following the recommendations of Aksnes and Ohman (1996) I collected up to 20 replicate samples at each site. However, the proliferation of negative mortality rates and a statistical power analysis (Chapter 2: [2.4.5](#)) demonstrates that replication will not alleviate the violation of assumptions nor increase accuracy. Rather than concentration of effort on a single location, it is recommended that sampling should be dispersed spatially and temporally. The mean instantaneous mortality over a larger scale has a greater chance of smoothing out perturbations from constant recruitment.

The SPM, in conjunction with molting rates observed through incubations, provides more meaningful values than previous vertical methods. Uncomplicated methods are needed to build databases for cross regional comparison and coupling of zooplankton populations to higher trophic levels. The batch incubations can easily be added to the cruise itinerary, and with it the population dynamics of copepods can be derived.

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## **BIOGRAPHY OF THE AUTHOR**

Cameron Thompson was born in Paget, Bermuda on January 14, 1985 to parents Lisa and Michael. Although, he grew up in the agricultural community of Kinderhook NY, his father's family is Bermudian. The many trips back to that tiny island in the middle of the Atlantic helped inspire him to pursue a path in marine science and policy. Cameron's interest in the natural environment and intersection with society was cultivated while spending summers on Lake George in the heart of the Adirondacks. While there he gained experience outside academia as a camp counselor and later a wilderness trip leader for groups of teenagers. This avenue of his life culminated with a 5 week backpacking trip during the summer of 2008 in which he led a group of teens to summit all forty six high peaks in the Adirondack mountains.

By this time Cameron had completed his high school and undergraduate career. He received his high school education from LaSalle Institute in Troy, NY, graduating in 2003. While at the Catholic military school he earned the distinction of going without a rank for the majority of his senior year, only receiving it back in time for the graduation ceremony. Throughout highschool Cameron ran for the cross country team, along with both the indoor and outdoor track teams; he wasn't very good, but managed to keep up the hobby to the present. He then attended the State University of New York at Geneseo in 2003 and obtained his Bachelor of Science degree in Biology in 2007.

Cameron's experience outside of academia includes leading wilderness trips as well as several field technician positions. As an intern in 2006 he worked at the Bermuda Aquarium and participated in sea turtle research. His work with sea turtles continued in 2008 as an intern for Mote Marine Laboratory in Sarasota, Florida, where he monitored the nesting beaches. After that experience Cameron headed inland to become a research technician at Del Rio, Texas in 2009. His work in the desert shrub land was on the endangered black capped vireo, a small handsome bird with a pleasant song. Cameron's

work with the sea turtles and black capped vireo convinced him to never work with another endangered species.

Starting in August 2009, Cameron was enrolled in the School of Marine Science's graduate program at the University of Maine. His time as a graduate student will inevitably come to an end, and his next steps may have to follow the Bermudian motto: *Quo Fata Ferunt*. Cameron is a candidate for the Master of Science degrees in Marine Policy and Marine Biology from the University of Maine in December, 2012.